THE CAPUCHIN MONKEY AND THE CAATINGA DRY FOREST: A HARD LIFE IN A HARSH HABITAT

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Preface

The text of this thesis does not exceed 80,000 words (or 350 pages) and it has not been submitted for any other qualification to this or any other university. This thesis is the result of my own work, sweat, blood and tears, and includes nothing which is the outcome of work done in collaboration that is not explicitly stated. All of the photos were taken by the author.

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'Of man's life, his time is a point, his existence a flux, his sensation clouded, his body's entire composition corruptible, his vital spirit an eddy of breath, his fortune hard to predict, his fame uncertain. Briefly, all the things of the body, a river; all the things of the spirit, dream and delirium; his life a warfare and a sojourn in a strange land; after fame, oblivion. What then can be his escort through life? One thing and one thing only, love of knowledge.'

Marcus Aurelius (121-180)

Acknowledgements

I thank my mum, Antônia Marlene de A. Moura, for everything, for always having a smile and good humour during all the adversities she has endured in this meaningless valley of tears; and my father, Mozart M. Brandão, despite his crushing ways of rising us that will be forever entrenched in myself, my brothers and my sisters. But, in his idiosyncratic way he loved and cared for everybody. Alirio, Wellington, Christiane and Lucila, I do love you even though I always look so apart and silent. And so I thank my shattered family and pray that one day we may be as one happy bunch of monkeys- a normal family!

Thanks to P. Lee (Pili) for all the help and for believing in a foreign student that hardly could speak English... Perhaps I can best express my profound thanks to Pili by stating that this thesis would not exist without her patience and sufferance during the writing up with so many missed deadlines. And to my first supervisors, Carmen Alonso and Alfredo Langguth, who taught me so much about science and primates I also have a profound debt. Thank you for everything.

I thank Henara Costa and Joe Murray, for so many good moments, for our football matches, the chess, cinemas, for proof reading one chapter and, of course, for the good food! You are my best friends! How can I convey how much I appreciate our friendship? Perhaps by borrowing the lines of the greatest bard: "*So long as men can breath, or eyes can see; So long lives this, and this gives life to thee.*" One day we will be dust and just a fading memory, but these lines will give life to ourselves, albeit forever buried in the vaults of UL.

Charlotte Peel, thank you for all the wonderful moments, for all the happiness we shared. You are special and no amount of words would express this enough!

I thank the expertise of Rudolph 'Madureira' with the photos, Nancy Priston for her advice with the english and also for not beating me up when she caught me in the act of 'crop raiding' the wonderful strawberries she left in the office...

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Finally, thank you for bothering to read these long bla bla bla and please read all of the thesis and may the force be with you!

SUMMARY

The capuchin monkey and the Caatinga dry forest: A hard life in a harsh habitat

Antonio Christian de Andrade Moura

This thesis explores the seemingly simple problem of how a rainforest-dwelling primate, *Cebus apella libidinosus*, manages to survive in the Caatinga dry forest of north-eastern Brazil, a harsh habitat that poses a series of extreme ecological challenges for survival. Albeit a simple question, it unfolds into more complex questions regarding how ecological pressures might drive brain evolution and intelligence in primates.

Although there is no "best" hypothesis to explain the evolutionary brain enlargement in higher primates, fine-grained analyses of ecology, such as those presented here provide insights into how different species deal with ecological problems that might require cognitive solutions. Capuchin monkeys are an ideal model for this inquiry. They occupy diverse habitats, and they have proven to be a cognitive puzzle. They are the only monkey to approach great apes in their ability to use tools, but apparently lack the prerequisite mental capability to understand cause and effect.

The Caatinga dry forest poses a series of ecological challenges for mammals in general and primates in particular, and these are detailed in this thesis. This is the first general study of mammalian abundance and distribution in Caatinga habitats, with special reference to *Cebus*. I present several innovative methods for assessing plant and invertebrate biodiversity, as regards foods for the *Cebus*. The study population of capuchin monkeys faced more frequent and longer periods of food scarcity than does any other known capuchin population. However, the *Cebus* in the Caatinga circumvent the ecological constraints of low plant food availability through their proficient foraging style (destructive foraging) and through their cognitive abilities, reflected in this population's extensive and intelligent use of technology.

I suggest that Old World monkeys and capuchin monkeys have undergone differential selective pressures, with 'Machiavellian intelligence' being a more prominent aspect in the brain evolution of baboons and macaques, while extractive foraging was a more important selective pressure for capuchin monkeys. The evolutionary brain enlargement observed in hominids is suggested to be a legacy of extractive foraging and that capuchin monkeys are excellent models for understanding the factors leading to brain enlargement. This thesis is concluded as an endeavour into understanding the selective forces and concatenation of events that culminated with the evolutionary brain enlargement seen in the hominins.

CONTENTS

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The female Cara-branca walking on the sky. The pods are from Anadenanthera colubrina.

Chapter I

GENERAL INTRODUCTION

This thesis was born from curiosity: to find out how a tropical rainforest primate dweller, such as the capuchin monkey, could survive in the Caatinga dry forest, a harsh habitat that poses a series of extreme ecological challenges for survival. This is a simple question, yet it unfolds into a much more complex panorama with important implications for understanding how ecological pressures might drive brain evolution and intelligence in primates. From a cognitive point of view the exploitation of a semi-arid environment, with a mosaic distribution of food resources and a relatively unpredictable pattern of fruit availability, seems to exert a higher selective pressure than a rainforest environment, which is a richer and relatively more predictable habitat. Perhaps the inherent unpredictability of more arid environments and the ephemeral distribution of food resources were important factors selecting for larger brain size in primates and particularly hominids (Elton *et al.*, 2001; Parker and Gibson, 1979; Potts, 2004a,b). Although the link between ecology and brain evolution is attractive and seems intuitively correct, this relationship is overly simplistic and other selective pressures could have played a more prominent role in the evolution of primate brains.

The tangled, the untangled and the lost beginning of primate brain evolution

Among mammals primates have unusually large brain relative to body mass, but the factors selecting for larger brain size are yet poorly known and are debatable (e.g. Iwaniuk and Arnold, 2004; Milton, 1988; Tomasello and Call, 1997). Recently,

Potts (2004a) suggested that the environmental challenges of a drier habitat in Africa and a frugivorous diet were key components shaping the cognitive abilities of great apes and last common ancestor with the hominins. He hypothesised that these variables worked synergistically with social variables, such as social learning and group structure, driving cognitive evolution in great apes. Indeed, experiments with starlings (*Sturnus vulgaris*) indicate that environmental unpredictability seems to exert greater selective pressure for social learning (Rafacz and Templeton, 2003) and perhaps it could select for increasing brain size and intelligence.

The causal factors responsible for the larger brain size of primates are difficult to pinpoint, however. The above suggestions are rooted in the hypotheses' predictions that the location of dispersed food resources in time and space is cognitively demanding and could be seen as the initial kick for the evolutionary increase of brain size among primates and other mammals (Clutton-Brock and Harvey, 1980; Milton, 1981).

Nevertheless, as cogently argued by Cheney and Seyfarth (1990), the challenge of exploiting widely-dispersed food resources may lead to increased intelligence, not simply because of the difficulty in finding food; instead the ecological complexities placed an increased selection on social skills, including the ability to cooperate in defence of resources and formation of alliances. A complex social network poses a strong selective pressure for solving the day-to-day social problems and a greater reliability on learning from others. The ways that monkeys, and primates in general, manipulate each other to solve social problems is much more sophisticated, frequent and with immediate selective consequences than are pressures to finding food. The social brain hypothesis (Dunbar, 1998) or Machiavellian intelligence (Whitten and Byrne, 1988) suggest that social challenges pose more complex and demanding problems on an animal than those that result from the

challenges of finding food. This is not to say, however, that ecological factors are unimportant. Indeed, since ecology determines the social context (see Dunbar, 2003), ecological factors lie at the heart of cognitive evolution. The question is whether there is further, direct effect of ecological problem-solving on aspects of cognitive evolution, such as those associated with technology.

In recent years there has been an accumulation of evidence suggesting that the intricacies of social life are the main selective force driving intelligence and brain evolution in primates (e.g. Bergman *et al.*, 2003; Kudo and Dunbar, 2001; Dunbar, 2003), dolphins (Connor *et al.*, 1999) and even in birds (Burish *et al.*, 2004). Yet, methodological problems in studies testing hypotheses for brain enlargement, at least in primates, suggest prudence in choosing any particular hypothesis to explain primate cognitive evolution (Deaner *et al.,* 2000). Recently, Reader and Laland (2002) argued for multiple selective forces for brain enlargement and suggested that ecological factors may have exerted a higher selective pressure on primate brain evolution than did other variables.

Most of these "tests" of brain evolution use a great number of data points of social and ecological variables correlated with specific indices of intelligence (e.g. neocortex ratio) or other measures of brain size, and although these test have considerable value in generating and testing specific hypotheses, they do have shortcomings (e.g. Deaner *et al.*, 2000). For example, Gibson (2002) highlights that the use of neocortical ratio as a measure of intelligence does not take into account that fact that other brain parts also contribute to various aspects of learning and memory. Moreover, these tests are correlational and as such do not allow the formulation of firm conclusions about causality (see Dunbar, 2003).

Regardless of which was the main selective pressure for brain enlargement, a key attribute of a larger brain is behavioural malleability and the capability to

innovate in new ecological or social situations (see Reader and Laland, 2002). In this sense, the making and using of tools to solve feeding problems is a remarkable facet of intelligence and correlate with relative brain size both in primates (Reader and Laland, 2002) and birds (Lefebvre *et al.*, 2002). Overall, primates present higher frequencies and variety of tool use than do other animal groups (Beck, 1980; Essock-Vitale and Seyfarth, 1987). In more unpredictable environments, tool use during food bottleneck periods could be an essential component of survival (Yamakoshi, 1998). The use of a single population of one species, as in this thesis, obviously only contributes to developing questions that can then be tested comparatively. When a population throws up novel behaviour, however, this points the way to new insights which can then be developed from the larger comparative dataset.

Comparison between species in tool use activity, and possible association with group size and social complexity, and ecological variables (feeding strategies) could provide meaningful insights into the causal mechanism leading to evolutionary brain enlargement. Unfortunately, however, these comparative studies in different species of monkeys in relation to tool use are still lacking. Nevertheless, studies of same species living in different environments and comparisons of similar species on cognitive performance reveal how habitat and feeding ecology can affect intelligence and anatomy of particular brain structures. For instance, Pravosudov and Clayton (2002) compared memory and brain in two populations of food-storing birds (*Poscile atricapilla*) living in areas with milder and harsher winters. The population from a harsher habitat (Alasca) had a relatively larger hippocampi with more neurons than the population originating from habitat with a milder winter (Colorado). Similarly, Platt *et al.* (1996) compared golden lion tamarins (*Leontopithecus chrysomelas*) and Wied's marmoset (*Callithrix kuhli*) on spatial and visual memory. Usually tamarins performed better in long retention-interval tasks (> 24 h) than marmosets. The authors

hypothesised that these species posses different visual-spatial memory, probably an adaptation for their particular feeding ecology. These kinds of studies can provide a basis for a better understanding of between-species differences in brain structures and to test functional hypotheses (see Shettleworth, 2003).

Tool use and confusions

In primates the use of feeding tools is restricted to great apes, baboons, macaques, capuchin monkeys (*Cebus* spp.) and occasionally some guenons (Beck, 1980; Yamakoshi, 2004). However, until now the only primate species to show customary[1] (*sensu* McGrew and Marchant, 1997) use of feeding tools in wild were chimpanzees and orangutans (van Schaik *et al.*, 1999; Yamakoshi 2004). Explanations for the lack of consistent tool use in wild non-human primates have been linked to an arboreal life style which limits contact with potential tools, i.e. stones, and could make it difficult or dangerous to manipulate detached objects in this context (Visalberghi, 1987; Anderson, 1990; Yamakoshi 2004) and to ecological constraints. For instance, Beck (1980) suggested the low availability of food or high predation risk would reduce the time available for manipulative activities that could act as precursors to tool use. More recently, van Schaik *et al.* (1999) and van Schaik and Pradhan (2003) suggest that the almost complete absence of habitual use of feeding tools in non-human primates was a question of a lesser intelligence in relation to great apes. They argued, supporting their argument with the classical works of Visalbergh and her group (e.g. Visalberghi and Limongeli, 1994,1996), that monkeys do not have understanding of the causal relations between tool use and the problem to be solved,

[1] McGrew and Marchant (1997) delineate four levels of tool use: 1) Anecdoctal- unique or rare events that show the possibility of an act, but are subject to alternative interpretations; 2) Idiosyncratic- events exhibited with relative frequency by only one individual; 3) Habitual- events repeated by several individuals, but could be fad or context-specific; 4) Customary- regular events by all appropriate members of a group and it can be seasonal or age-specific.

but this is a very debatable point (Tomasello and Call, 1997). I will return to these points and provide more details in Chapter VI. What is significant here is that, of all of the primate species, only capuchin monkeys come close to matching the great apes in frequency and diversity of tool use. In captivity, capuchin monkeys have been shown to use sticks as probes for ant-gathering (Westegaard *et al.*, 1997) and honey extraction (Levallee, 1999); they can use tool sets in sequences, similar to those of chimpanzees (Westegaard and Suomi, 1993); they use sticks as a digging tool when searching for hidden food under the soil (Westegaard and Suomi, 1995); hammer-and-anvil stones to crack nuts (Visalbergh, 1990) and they even manufacture stone tools (Westegaard and Suomi, 1994). The capuchin monkeys studied by Westegaard and Suomi in captivity apparently were able to perform most of the tool activities observed in wild chimpanzees.

Why are capuchin monkeys so prone to tool use? Even when comparing the abilities of capuchin monkeys at using tools with those of baboons and macaques, capuchins still stand out in their preponderance of tool use and promptness to solve tool-related problems. For instance, Chevalier-Skolnikoff (1989) highlighted that capuchin monkeys solve feeding problems using tools at a rate 50 to 100 times higher than do baboons and macaques, and Tokida *et al.* (1994) noticed that *Macaca fuscata* was much slower than capuchin monkeys at solving a tool-stick problem. In a comparative study of manipulative abilities of 74 primate species, Torigoe (1985) found that only capuchin monkeys and chimpanzees stroked an object against the substrate. Apparently the underlying explanation for these impressive abilities in tool use lie in the complex manipulative capabilities of capuchin monkeys and great apes, which are probably adaptations for extracting embedded food resource, i.e. the

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extractive foraging[2] theory put forward by Parker and Gibson (1977) and Gibson (1986). They argued that the food eaten by most primates requires considerable manipulation before being eaten and these expanded sensori-motor capabilities are reflected in neocortical expansion. They further reasoned that species with an eclectic diet and with the habit of exploiting a wide range of seasonally-limited embedded food resources, but who lack anatomical specialisations for exposing these hidden resources, face a kind of ecological problem that can be cognitively demanding. To solve this type of problem requires complex sensori-motor coordination and intelligence, and this could induce the evolutionary enlargement of the brain and specialised tool use observed in some primate species.

The extractive foraging theory has an embedded elegance for explaining brain evolution. The brain is an expensive tissue and its growth and maintenance require high-quality food (Aiello, 1997; Foley and Lee, 1991); and those foods obtained through extractive foraging tend to be 'premium' foods with a high content of energy and protein (Gibson, 1986). Moreover, as youngster do not have the capabilities and strength of adults for obtaining hidden food, thus there is a selective pressure for social learning and perhaps an extended juvenile period (e.g. Joffe, 1997). Altogether these variables probably influence the cognitive evolution of hominins (Parker and Gibson, 1979).

However, the extractive foraging hypothesis has been dismissed by Dunbar (1995; 1998), since he did not find any relationship between neocortex size and level of extractive foraging. Furthermore, this hypothesis has serious limitations, especially for explaining the great cognitive enhancement shown by apes in the social domain and their more sophisticated mental capabilities in relation to monkeys (see Byrne

[2] Accordingly to Gibson (1986; p. 96) extractive foraging 'means feeding on foods that must first be removed from other matrices in which they are embedded or encased', i.e. food that is not visually apparent and requires time and energy to became available.

1997). Pinpointing the reasons for a larger brain size in primates and the processes leading to it has been a difficult task. The extractive foraging theory, despite the strong criticism, has recently moved back into the spotlight of cognitive evolution for hominins (Singleton, 2004; Yamakoshi, 2004). All these hypotheses explaining why primates have larger brain size and the evolution of intelligence are conjectural - they cannot be tested- and probably there is no 'best' explanation. Nevertheless, I do believe that extractive foraging hypothesis could be a fruitful approach to explain tool use and some aspects of brain evolution, and perhaps our evolutionary success.

Homo sapiens is the most invasive, common and widespread species on Earth and our triumph, as a biological species, is directly linked to a larger brain size and an enhanced ability to use and make tools. Yet what are the prime movers for the origin and evolution of human tool technology and which promoted an increase in brain size, remains an unsolved evolutionary puzzle that has fascinated scientist for centuries (Parker and Gibson, 1979; Westergaard and Suomi, 1995; Ambrose, 2001; Elton *et al.*, 2001; Balter, 2002) and I suggest that it could be a legacy of extractive foraging.

For understanding the evolution of tool technology, however, it is necessary to comprehend the pressures that could have promoted tool use. If extractive foraging is the foundation of tool-use behaviour, it is reasonable to assume that the most extractive foragers will be the eager tool users. Among primates, capuchin monkeys spend up to 44% of their foraging time engaged in extractive foraging on a wide range of food resources (Terborgh, 1983); they are extractive foragers *par excellence*. Yet all of the records of wild capuchins using tools have been anecdotal (*sensu* McGrew and Marchant, 1997) and undermine this hypothesis. However, a specific prediction of the extractive foraging theory - that the conditions selecting for increased tool use and intelligence would be found in populations of *Cebus* and chimpanzees living in 'unproductive' and highly-seasonal habitats and that these populations would present

high levels of intelligent tool use, i.e. flexible use of tools with an understanding of cause and effect (Parker and Gibson, 1977) - has yet to be evaluated. The key point is that is until now we are lacking studies on capuchin monkey groups living in a harsh environment, where the use of feeding tools could have direct implications for their survival. Hence, the following are the ultimate objectives in this thesis:

1-To assess if a harsh environment could be an important selective pressure driving tool use and intelligence;

2- To argue that tool technology is not better explained by social intelligence; instead to propose that extractive foraging could be an alternative explanation;

3-Finally, to argue that in order to understand the factors shaping the cognitive evolution of hominins, the New World monkeys, and particularly capuchin monkeys (*Cebus* spp.), are excellent models. The study of *Cebus* in dry habitat is a unique opportunity to understand the survival strategy of a primate usually found in wet forest when faced with a harsh environment.

To achieve these aims, I studied a population of *Cebus apella* living in the dry forest of Northeastern Brazil. This is the first ecological study of capuchin monkeys living in a harsh and challenging habitat. A primary goal in this thesis is a detailed description of this dry habitat; of the foods available to the capuchins; of their spatial use of this habitat; and to explore how the diversity and seasonal scarcity of resources influences their foraging.

This thesis, then, is a long argument. First I will highlight the unpredictable nature of rainfall and describe how semi-arid is the Caatinga (Chapter II) and then discuss how this affects plant diversity and the production of food resources (Chapter III). These ecological factors have a striking impact on the mammalian community in general and particularly on the primates. Areas with a higher biodiversity tend to have a high productivity (Rosenzweig, 1995), i.e. food availabitility. A recent study by

Armbrecht *et al.* (2004) shows that twig-inhabiting ants, an embedded resource for capuchin monkeys, are more diverse in areas with higher biodiversity. Thus, I suggest that the density of primates in the Caatinga will be higher in habitats with high diversity. How these features of low diversity impact on the abundance and distribution of primates, including capuchin monkeys, is explained in Chapter IV.

In Chapter V, I analyse the feeding ecology of the monkeys and try to answer the questions of how they survive in this area, and how the difficulties of finding food in this environment could exert selective pressures for increased use of intelligence and technology. In an environment like the Caatinga, tool use could be very important for survival and in Chapter VI this will be analysed in detail. The use of a stone to open a nut could reduce the time taken to open it, which ultimately means more food is eaten in less time, leading to an improvement in the returns from foraging activities. In chimpanzees, tool use greatly facilitates feeding efficiency during times of food scarcity (Yamakoshi, 1998). Thus, I predict more frequent tool use by *Cebus apella* in the Caatinga, especially during the dry season, when they potentially increase the frequency of tool use and use more types of tools in order to reduce their time foraging on particular foods, and thus optimise their food intake during drought. Finally, I will make inferences about the evolution of the hominin line and the adaptations of Old World monkeys with regard to brain evolution in the final discussion chapter.

Chapter II

GENERAL METHODS

INTRODUCTION

In this chapter, I give a general overview of capuchin monkeys, of the Caatinga dry forest and a description of the site where the study was carried out. Finally I delineate the main methods used to assess biodiversity in the area and provide a general description of the statistical methods employed for analysing the data collected. Some specific methods and analyses, e.g. censuses, insect collection, are described in relevant chapters and therefore are not dealt with here.

Capuchin monkeys: characteristics, taxonomy and distribution

Capuchin monkeys, genus *Cebus*, are medium-sized New World primates weighing about 3.5 kg (males) and 2.5 kg (females) with a diet composed mainly of insects and fruits (Ford and Davis, 1993; Freese and Oppenheimer, 1981). They live in multi-male multi-female societies with an alpha male and alpha female (Fedigan, 1993; Izawa, 1980; Janson, 1984; Perry, 1996). *Cebus* is a very wide-ranging genus of New World primates. Today four or possibly five species are recognised: *C. capucinus*, ranging from Honduras to extreme northern Colombia; *C. albifrons* found in northern west South America and the upper Orinoco river basin and over a vast area of the upper Amazon basin extending as far north as northern Bolivia; *C. olivaceus* (=*C. nigrivittatus*), found in northern South America in the Orinoco River basin and north of the lower Amazon and Negro River basins in the Amazonian forest; *C. apella* found from extreme northern South America to northern Argentina (Freese and Oppenheimer,

1981; Mittermeier *et al.*, 1988) and *C. kaapori,* a recently described species found in eastern Amazonia (Queiroz, 1992), but which may be just a regional form of *C. albifrons* (Masterson, 1995).

Hershkovitz (1949) divided the *Cebus* into 2 groups based on the presence of a distinctive frontal tuft of hair on the head (the tufted group composed only of *C. apella*) or its absence (untufted group, all the other species). However, the taxonomy of the group is still poorly understood, mainly with respect to *Cebus apella*, due to great individual variation (Hill, 1960; Torres, 1988).

Among the Neotropical primates, *C. apella* has the widest geographical distribution as noted above. This species occurs from extreme northern South America to northern Argentina (Freese and Oppenheimer, 1981), occupying a great variety of habitats, from evergreen rainforest to dry woodlands. Their biological success can be attributed to the following features (shared with other *Cebus* species to differing degrees):

1. Morphological adaptations of teeth, jaws and masticatory musculature (Masterson, 1997; Anapol and Lee, 1994), which enable consumption of palm nuts and hard-shelled fruits during periods of food shortage (e.g. Robison, 1986; Terborgh, 1983). Among the capuchin monkeys, *C. apella* presents a more robust build and thicker tooth enamel.
2. Their characteristic foraging behaviour (linked to the above features) called destructive foraging (Terborgh, 1983; see Chapter V for more details) in which they strip bark off trunks, break branches or bite them open while looking for animal prey. This type of foraging allows them access to hidden prey in tough substrates.
3. Their cognitive capabilities reflected by their intensive tool use, shown in captive studies (reviewed by Visalbergh, 1990) as well as in the wild, albeit in an anecdotal

way (Langguth and Alonso, 1998; Rocha *et al.*, 1998). Their cognitive abilities are also shown in their proficient behavioural techniques for preying upon social insects (Janson and Boinski, 1992).

These key features allow *C. apella libidinosus* to live in the *Caatinga* forest, which is a very dry tropical forest located in Northeastern Brazil.

Tropical dry forests and the Caatinga

Dry forests are characterised mainly by extreme seasonality in rainfall patterns. Usually the average annual rainfall is less than 1600 mm, there is a marked dry season of three or more months and most of the vegetation is deciduous during the dry season (Gentry, 1995; Murphy and Lugo, 1986). Tropical dry forests differ from savannahs in their predominance of trees with a relatively continuous canopy, a virtual lack of a grass herbaceous layer, and they usually occur in richer soils and drier conditions than savannahs (Pennington *et al.,* 2000).

In the Caatinga dry forest of Northeastern Brazil, the climate is characterised by low and irregular rainfall, which causes a severe water deficit, and great variation between years in the amount of rainfall. Extreme drought (zero rainfall) for a year or more is not uncommon, especially during *El niño* periods when droughts can last for more than two years (Sampaio, 1995). The average yearly precipitation in this region is about 800 mm, but in certain localities it may be below 300 mm (Reis, 1976).

The *Caatinga* formation is a deciduous tree-shrub forest vegetation, covering almost 1,000,000 km^2 in Northeastern Brazil and is the third largest biome in Brazil (Fig. 1). The name *Caatinga* was given by Tupi indians and means white (*tinga*) forest (*caa*). Possibly, the name is an allusion to the dry season, when almost all trees lose their foliage and the bare branches become very light in colour.

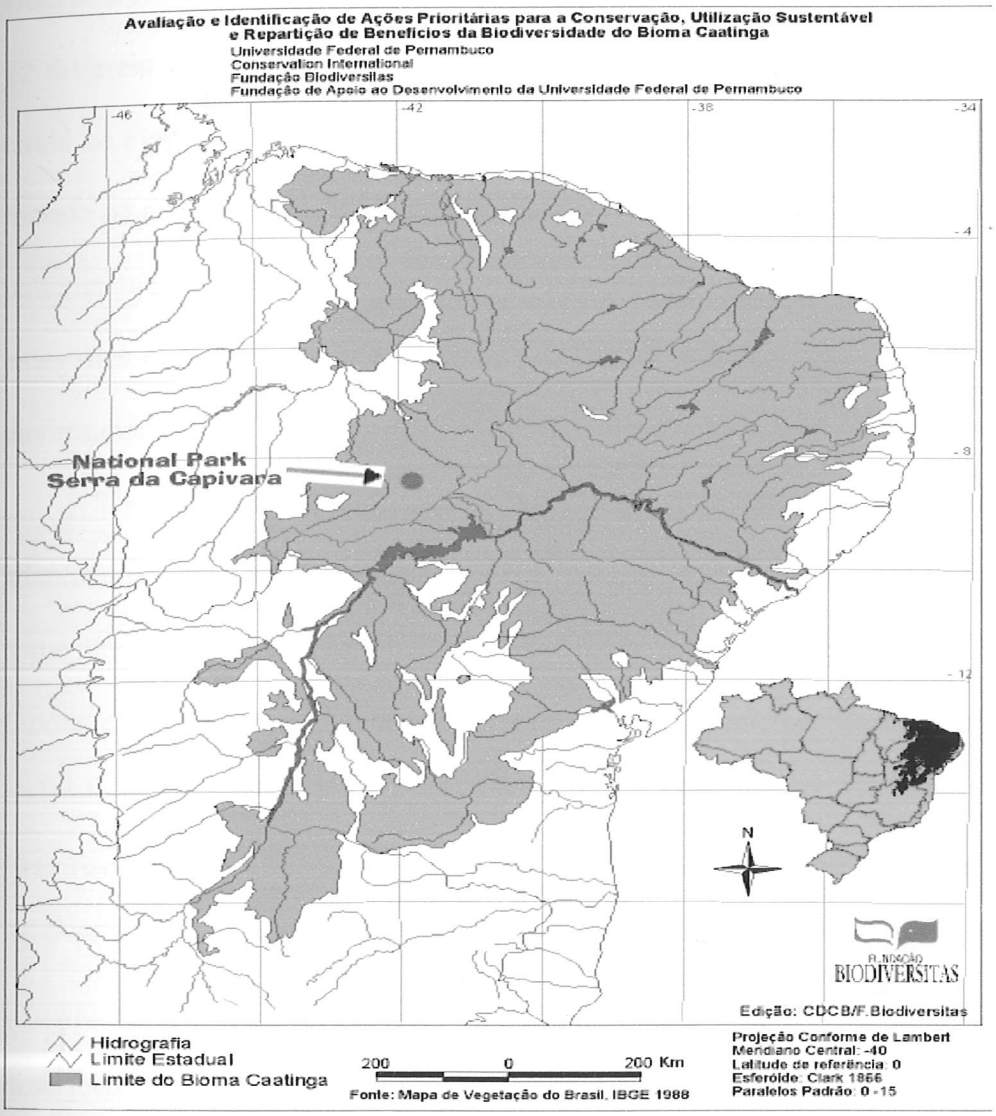

Figure 1. Map showing the area encompassed by the Caatinga biome and location of Serra da Capivara National Park.

Local people classify the Caatinga vegetation into two types: *alta* (high) tree forest of 10-15 m in height, and *baixa* (low) scrub, a thorn-scrub open vegetation about 3-6 m height. Some tree genera found in Caatinga *alta* type are *Myracrodruon, Hymenaea, Caesalpinia, Acacia, Anadenanthera, Zizyphus, Enterolobium* and the cacti *Cereus jamacaru*, which can attain up to 10 m in Caatinga *alta*. The Caatinga *baixa* is composed predominantly of *Mimosa, Jatropha, Cnidoscullos, Senna,* some cacti (*Opuntia, Pilosocereus*) and spiny bromeliads (*Encholirium spectabilis* and

Hohenbergia sp.). Andrade-Lima (1981) classified the vegetation of the Caatinga into 12 different types based on species composition and height, and suggested that there could be even more vegetation types. In fact, the Caatinga is better viewed as being a mosaic of different vegetation types, which are locally determined mainly by rainfall patterns and soil conditions. As noted below, and in Chapter III, I restrict my habitat categories to four, which correspond to major landforms or geological features in the environment.

The vegetation in this biome exhibits many morphological and physiological adaptations for the unpredictable rainfall patterns (Mares *et al.*, 1985). For example, some plant species have barrel trunks (e.g. *Cavanillesia* sp., *Ceiba* spp.) , tuberous roots (*Spondias tuberosa*) and other modifications to store water. The Caatinga has about 180 endemic plant species (Prado and Gibbs, 1993). Nevertheless, contrasting with other Brazilian habitats, Caatinga contains only two species of endemic mammals: the rocky cavy (a caviide rodent: *Kerodon rupestris*) with a wide distribution in the Caatinga (Nowak, 1999), and the spiny rat (Echymyidae: *Preochymys yonenagae*) a recently described species with a more restricted distribution to the sand dunes of the middle São Francisco river (Rocha, 1995). Some studies have described the mammalian fauna as being one of the poorest assemblages of the tropics (Mares *et al.*, 1985; de Vivo, 1992; see Chapter IV).

Mares *et al.* (1985) suggested two hypotheses for the lack of more endemic mammal species: 1-The Neotropical region has undergone several cycles of climatic fluctuations, accompanied by corresponding changes in vegetation; during moist phases the arid "refuges" were not large enough to support viable populations of arid adapted mammals; 2- the irregular and lengthy droughts prevented adaptations to arid conditions, i.e., several generations of small mammals would experience a strong

selection for the lengthy drought, while in years of abundant rain the new generation would have an opposite selection, thus it would be difficult for any adaptation for arid habitats to be consolidated in the genetic pool of the population.

It is possible, however, that other endemic species simply went extinct before becoming known to science. I think the most plausible candidate for such a possibility is the rodent *Juscelinomys cadango*, a new genus and species discovered in the dry Cerrado during the construction of the Brazilian capital, Brasilia, in 1960. However, despite extensive searches no other specimen has been found since then (Nowak, 1999). The dry forests are fragile, and Caatinga has suffered almost five hundred years of cutting and burning agricultural practices, which might have caused the extinction of many unknown species.

A long history of disturbance and possible effects on the fauna and flora

Humans have inhabited South America for more than 10,000 years and it is likely that these early inhabitants had impacts on the wildlife. However, with the arrival of the European colonisers in the XV century, bringing new technologies and a 'savage' greed for exploitation of natural resources, their impact on the ecosystems was deeper and much more acute. In Brazil, the Atlantic forest was at the front line of the havoc wrought by the early Europeans. In the middle of the XVI century, the fires and destruction of forest were already a matter of concern, yet the destruction continues to the present, as so elegantly and poignantly described by Dean (1995).

In contrast to the Atlantic forest, the settlement of the vast Caatinga was mainly by cattle ranchers in the XVI and XVII centuries (Coimbra-Filho and Gusmao, 1996; Dean, 1995). The subsequent growth of farms, coupled with clearing and burning of the land, had dire consequences for the native plants and animals in the

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area. More than eight decades ago Neiva and Penna (1916), exploring the Caatingas of Piaui and Bahia, commented on how rampant fires over extensive areas and the intensive cutting of trees (for charcoal, to gather honey combs etc) were altering the wildlife abundance. Webb (1974) went on to suggest that the present-day vegetation formation is a secondary forest originated from the past human disturbance. He recounts how, in over 1300 km of field travel in Northeastern Brazil during 1960-1963, the old inhabitants of the area clearly remembered the vegetation being taller, denser and with thicker trees. Coimbra-filho and Gusmao (1996), in a thorough review of historical documents on the occupation of the Caatinga and *in situ* observation of human impacts on wildlife, endorse the ideas of Webb. They argue that Caatinga was once a taller and not so strikingly dry forest as nowadays. Indeed, the uncaring activities of humans, through the axe and fire, opened the way for the decimation of the fauna and flora and nowadays the vegetation, and its dependent consumers, is a mirror of the combined effects of human disturbance, soil and climate.

How many species disappeared as a consequence of human activity and how altered, in terms of forest composition, structure and functioning is the Caatinga? In the Atlantic forest, despite 400 years of even more intensive disturbance than in the Caatinga, there is no record of a species going extinct (Dean, 1995). Thus, that is a difficult question to answer, although logic dictates that species have gone extinct and some evidence points to a very altered structure of the forest as a result of the immense disruption by human activities. Nevertheless, as Dean (1995) points out, studies of natural history started only in the second the half of XVIII century, with a few admirable exceptions, and when those naturalists ventured into the wilderness they went by known routes, already used by the inhabitants and linking villages, farms and small towns in the interior. Ironically (but also a remarkable fact), all of the

natural grandeur that they observed was already from a disturbed ecosystem, yet with an extremely high biodiversity, and the many new species collected were probably those more resilient to disturbance and which escaped the fires. Indeed, Dean (1995) mentions a completely black macaw that had been described by numerous chroniclers from the XVII to XVIII century, but which was never described by science and he suggests that many more species probably went extinct as a result of forest conversion and fires. Dry forests are more vulnerable to disturbance than wet forest, since the successional process is slower (Murphy and Lugo, 1986) and the pioneer trees in dry forest produce wind dispersed fruit that usually are not eaten by vertebrates (Janzen, 1988), delaying even more the recovery of the forest. It is reasonable to assume that Caatinga suffered a greater loss in biodiversity than did the Atlantic forest.

Only the remoteness of an area worked as a guarantee for the preservation of the forest and its fauna. The place where I carried out my studies, the Serra da Capivara National Park, is located in a very remote area of South-eastern Piaui state and still harbours a rich wildlife, and some areas present almost pristine vegetation. It seems also to be the last area in the Caatinga where jaguars (*Panthera onca*), giant ant-eater (*Myrmecophaga tridactyla*) and white lipped peccaries (*Tayassu pecary*) co-occur (Wolff, 2001). I started my field study there in October 2000 and I left the area in March 2002.

Study site: Area, fauna and weather

The Serra da Capivara National Park located on the coordinates of 7^0 30' S and $41^0$30' W, covers an area of 129.953 ha. Four habitat types are distinguished in the southwest area of the park (see Chapter III for quantitative analyses of these) where the bulk of this study was carried out; these are also the main habitats occurring throughout the park. They are defined as:

- A sandstone plateau (about 500m above sea level), with a peculiar low stature vegetation (see Chapter III) accounts for about 65% of the Park (Fig. 2);
- Canyons of varying length and width dissecting the plateau on its border, accounting for about 15% of the park area. The vegetation inside these canyons was taller, in some trees reached up to 30m, these canyons were wetter and most of them had permanent or temporary water holes (Fig. 2);
- Cliffs (or *Cuesta*) separating the Plateau from the inter-planaltic depression (plains, see Fig. 2); the vegetation on the Cliffs was tall, and with very characteristic species such as *Tabebuia impetiginosa, Anadenanthera colubrina* and *Prockia crucis*. This habitat occupied about 10% of the area encompassed by the park;
- The plains had a medium-height forest (5 to 10 m): some species seemed to be unique to this habitat, such as *Tabebuia spongiosa* and *Calliandra depauperata*. Although being an extensive and important element of the landscape, it accounts for less than 5% of the park areas.

a.

b.

c.

Figure 2. Major habitat types in the Park Serra da Capivara: a- view of the Plateau and vegetation along the Cliffs; b- the forest inside the Canyon: even during the height of the dry season the trees there keep their leaves; c- a general view of the plains and plateau during the height of the dry season (Sept-Oct).

I did not evaluate the vegetation in this last habitat, since it accounted for a small area of the park, the monkeys I was studying hardly ventured in the plains and the vegetation was more disturbed and recovering. Emperaire (1984) in a detailed analysis of the geomorphology and associated vegetation, recognised up to eight different types of habitat encompassed by the Park, each with a characteristic vegetation type.

Fifty-seven mammals and 185 bird species have been identified in the park (FUMDHAM, 1998), including three species of primates: *Cebus apella libidinosus*, *Alouatta caraya* and *Callithrix jachus.* Some endangered mammals species such the three-banded armadillo (*Tolypeutes trincinctus*); greater anteater (*Myrmecophaga tridactyla*) and jaguar (*Panthera onca*), and birds, for instance the blue-winged macaw (*Ara maracana*), are also found within the park (Olmos, 1992). Possible predators of monkeys in the park are the jaguar, puma (*Felis concolor*), ocelot (*F. pardalis*), boa snake (*Boa constrictor*), and some species of hawks (e.g. *Buteo magnirostris*; *Heterospizias meridionalis*) that can predate the small marmoset. A larger eagle (*Geranoaetus melanoleucos*) also occurs in the park and could predate younger howlers and capuchin monkeys.

The majority of this study was done in the southwest area of the Park (Fig. 3), an area that was close (about 20 km) to the city of Sao Raimundo Nonato (SRN). This area had undergone considerable disturbance, chiefly in the plains and areas along the Cliffs. In the beginning of the XX century, Luetzelburg (1922) drew attention to the intense exploitation of trees in the Canyons nearby SRN, probably inside the present area of the park. He highlighted the fact that logging was so intense in some Canyons that they were almost treeless. Apparently, most of the vegetation in these Canyons had recovered (Chapter III). The sites of Baixa Grande, Oitenta and Jurubeba were farms bought by the FUMDHAM, a NGO responsible for the management and conservation of the Park. These areas were incorporated into the park, functioning as a buffer zone. They were bought in 1997, and the vegetation is a kind of successional mosaic; along the Cliffs there are a few places where the vegetation is almost pristine, while in other places most of vegetation is in process of recovery from past disturbance.

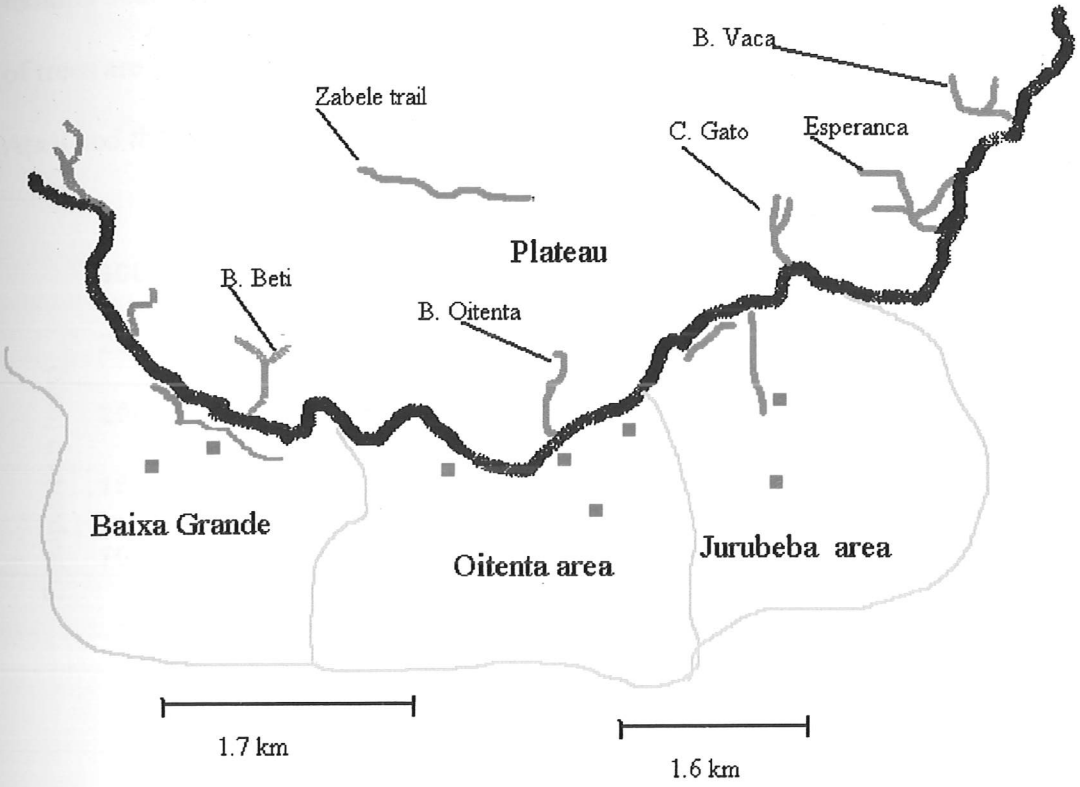

Figure 3. Highlights of the main study areas: Southwest part (Baixa Grande, Oitenta and Jurubeba), Centre of the Plateau (Zabele) and Southeast part (Esperanca and Baixao da Vaca Canyons). The red line represents the trails used for mammal censuses (details in Chapter IV), the blue squares are vegetation plots and the green represents Canyons (see Chapter III). The scale provides a rough idea of distance. For instance, the Zabele trail was about 17 km to Oitenta area and Esperanca Canyon was circa 15 km.

The rainfall regime in the Park is quite variable. Over a 50-year period, the average annual rainfall was 644 mm (data collected in Sao Raimundo Nonato), but there was a great irregularity in the amount of rainfall. For instance, in 1932 the total rainfall was just 250 mm and in 1948 it was 1131mm (Emperaire, 1984). The average annual temperature is 27^0 C. Overall the soils in the park are acid (pH 5) (Emperaire, 1984).

However, over a shorter period of time, closer to my study, the average annual rainfall was 781 mm (SD ± 177 mm, n= 7 years). A marked dry season of about 6

months occurs from May to the middle of October. During the dry season, over 70% of trees are leafless (Chapter III). The rainy season usually extends from November to April and the wettest month is March (Fig. 4)

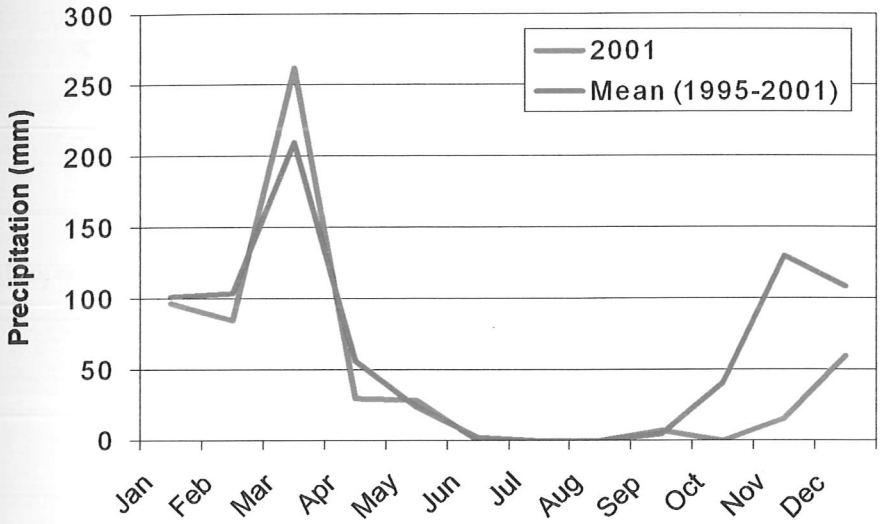

Figure 4. Annual rainfall in the area during the study and the average for seven years.

Considering just the year 2001, when most of this study was done, if I use Dunbar's (1992) definition of dry months as those with less than 50 mm of rain, the "dry" season would have been longer than usual at 8 months (Fig. 4). Studies of vegetation suggest that dry months are those with 60 mm or less of rainfall (e.g. Trejo and Dirzo, 2002; Clinebell *et al.*, 1995). Here, I have taken the periods from when the trees lose their leaves (May) until most of the trees begin to leaf again, which was in October. Thus I have a six-month dry period from May-Oct.

The rainfall variability from year to year was extremely high for the seven years data I analysed; the CV ranged from 98.2% to 154.8%. Even considering only the rainy months, the variability remains strikingly high (Fig. 2). I tested the

differences between the coefficients of variation among these rainy months using a test for homogeneity based on a chi-square distribution (Zar, 1996):

$$\chi^2 = \frac{\sum_{i=1}^{k} v_i V_i - \frac{\left[\sum_{i=1}^{k} v_i V_i\right]^2}{\sum_{i=1}^{k} v_i}}{V_p^2\left(0.5 + V_p^2\right)} \qquad \text{where} \qquad V_p = \frac{\sum_{i=1}^{k} v_i V_i}{\sum_{i=1}^{k} v_i}$$

and $v_i = k\text{-}1$; $V_i = SD/x$

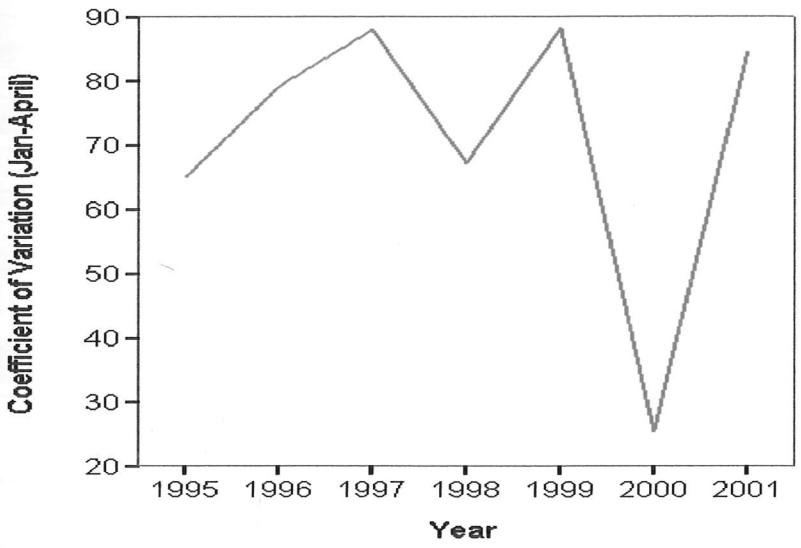

Figure 5. Rainfall variability as coefficient of variation for four rainy months (January to April). The difference among years is significant (χ^2= 15.9; df=6; p<0.02).

The extreme variability in rainfall pattern has a great impact on food availability in the area, which is probably reflected in the low abundance of mammals (see Chapters III and IV).

Assessing species diversity

Perhaps the simplest way to describe community and regional diversity is the use of species richness, i.e. the number of species observed. This is one of the most widely-used measure of diversity (Lande, 1996; Magurran, 1988; Stirling and Wilsey, 2001). Although simple and comprehensible, the species richness has an inherent dependence on sample size; the greater the area (or number of individuals) sampled, the higher the number of species. Moreover, the relationship between number of species and its abundance in a community has important biological connotations. This has long been recognised as a problem for comparing communities or habitats using just species richness (Hulbert, 1971; Stirling and Wilsey, 2001). For example, two habitats with equal number of species, but with differences in the abundance of a few species will be considered as "identical". Nevertheless, differences in the number of individuals counted in areas with similar size can indicate important biological patterns of local resource availability (e.g. food resources, water availability etc) or even more general evolutionary processes. Thus, comparing only species richness between communities can produce misleading results (Gotelli and Cowell, 2001). This limitation of species richness probably gave rise to diversity indexes. According to Hurlbert (1971) two main factors led to the creation of the diversity index: 1- the discrepancy in the structure of two collections with identical number of species and individuals; 2- the perception that the number of species and their relative abundance could be combined into an index including other properties of the community than just the number of species.

The number of different methods for estimating species diversity is enormous and comparisons of these different indices show inconsistencies in ranking of habitats and communities (Hulbert, 1971; Magurran, 1988; Krebs, 1999), or as Peet (1974) put it so succinctly "diversity, in essence, has always been defined by the indices used to measure it". These differences stem mainly from the differential weight put on species abundance or evenness by the numerous diversity measures, which has lead to the creation of a plethora of diversity indices and their accompanying critique (Hulbert, 1971; Magurran, 1988; Rosenzweig, 1995). Nonetheless, two diversity indices have proved robust to criticism and are presently the most widely used: the Fisher's alpha (α), a parametric index, which is based on the species abundance distribution; and the Shannon-Weaver (H')[1], a non-parametric index based on information theory, which is independent of species distribution models.

The Fisher's α was the first diversity index developed for interpreting the relationship between abundance (number of individuals) and species richness (Hairston, 1959). Fisher *et al.* (1943) when tabulating the number of individuals per species of nocturnal Lepdoptera, observed that a large number of species were represented by just one or less than five specimens, many species had less than 10 individuals and so on. Only a few species had a larger number of individuals in the collection. This frequency distribution produces a curve resembling a hyperbola. When the result were plotted as the log of # species against log of # individuals, the expected number of species holds only for the rarer species, but not for the commonest. Fisher reasoned that a logarithmic series, deduced from a negative

[1] The Simpson's index (D) is also a popular non-parametric index of diversity and independent of sample size, Lande (1996) highlight it as an excellent measure for diversity. This index was the first non-parametric index created as an alternative to the diversity indices based on species abundance distribution, such as log-series and log-normal (Krebs, 1999). However, most papers use a biased form of D (Σp_i^2); moreover, as D increases with *decline* of diversity, the commonly used transformations (1/D and 1-D) have a series of problems (for details see Rosenzweig, 1995). For these reasons and also since it is not so widely used as the Fisher's alpha and H' indexes, I decided not to use the Simpson's index.

binomial distribution, could provide the best fit for describing the species distribution. If the species distribution fit a log series then α can be calculated from the following equation:

$$S = \alpha \ln\left(\frac{1+N}{\alpha}\right)$$

where S= number of species and N= total number of individuals.

The value α is independent of the sample size, and thus values originating from different sample sizes can be compared (Fisher *et al.*, 1943). Although this index has the assumption of species abundance fitting a log-series distribution, it can be used even if the abundance of species does not fit the log-series distribution (Magurran, 1988; Rosenzweig, 1995). In her review of diversity indices Magurran (1988) describes a series of studies pointing to the advantages of the Fisher's α, and how its satisfactory performance in diverse circumstances should make it the first choice of diversity index. Indeed, Rosenzweig (1995) has championed the use of this index and stressed that the Fisher's α can accurately describe the relationship between area and species.

The Shannon-Weaver index (H') is based on information theory and it tries to summarise species richness and evenness in a single number (Magurran, 1988) that can be calculated from:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where $p_i = (n_i/N)$, and n_i is the # of individuals of the ith species and N is the total number of individuals. A t test was developed by Hutcheson (1970, quoted in Magurran, 1988) to compare two sites or habitats using the calculated H':

$$t = \frac{H'_1 - H'_2}{(\text{var } H'_1 + \text{var } H'_2)^{0.5}}$$

where:

$$\text{var}_t = \frac{\sum_{i=1}^{S} pi(\ln pi)^2 - \left(\sum_{i=1}^{S} pi \ln pi\right)^2}{N} + \frac{S+1}{2N^2}$$

From all of the diversity indices, the Shannon is the most widely used and popular among ecologists. Yet it is the most criticised index of diversity. For example, Whittaker (1972) pointed out the limitations of using H' in very speciose communities, when it could became inexpressive of the increasing diversity. Lande (1996) expressed the same criticism about a biased estimation in H' from speciose communities. Hurlbelt (1971), however, was the most acerbic critic and he emphasised that the Shannon index was of dubious value in any ecological problem. Nevertheless, the advantages outweigh these shortcomings. For instance, the Shannon index is relatively independent of sample size (e.g. Whitaker, 1972; Magurran, 1988), the proportional diversity measured is not strongly affected by rare species and it is the best index to measure the joint influence of species richness and evenness (Stirling and Wilsey, 2001). Moreover, H' follows a normal distribution, making possible to use parametric statistics including ANOVA (Magurran, 1988) and its wide use makes the Shannon index the most useful comparative empirical statistic of diversity (Stirling and Wilsey, 2001). For calculating H' values I used the program PC-ORD Version 4 (McCune and Mefford, 1999).

Statistical analyses

Throughout I prefer to use non-parametric statistics due to their simplicity and a relative independence of distribution types. I entered and analysed all data with the

SPSS statistical package version 9 for Windows and for some analyses I used Microsoft Excel. For data where I used parametric statistics, I checked the distribution of the variables using q-q plots and the Kolmogorov-Smirnov one sample test with a Lilliefors significance correction factor (Field, 2000). On rare occasions, I used parametric statistics when the distribution was not normal, even after 'normalisation'. In these cases, the population sizes were larger, usually N>> 50, and as the mean of samples from large populations whatever their distribution tend to converge to a normal distribution accordingly to the central limit theorem (Sokal and Rohlf, 1995; Zar, 1996), then the use of parametric statistics is acceptable.

For some analyses I needed to compare more than two samples and I used standard tests (parametric and non-parametric ANOVA). However, when using a *post hoc* test to identify a true difference among the sample means (multiple comparison tests) a significant result could appear just by chance, i.e. the probability of a Type I error (rejecting the null hypothesis when it is true) is higher, and increase directly with the number of tests performed. This problem has received a considerable attention and there are many statistical procedures trying to pinpoint the true hypotheses, yet among statisticians there is not yet a consensus about which is the best method (Lea, 1991; Saville, 1990; Sokal and Rohlf, 1995; Zar, 1996). Saville (1990) emphasised that the basic problem with these multiple comparison tests were the lack of consistency in the decision if two populations means differ.

Nevertheless, when using the Kruskal-Wallis non-parametric ANOVA, I decided to use the Bonferroni procedure for its simplicity and relative robustness (Field, 2000). The logic of this test is just to adjust the alpha level to the number of tests to be performed, thus lowering the probability of committing a Type I error i.e. $\alpha' = \alpha/k$, where k is the total number of comparisons (Sokal and Rohlf, 1995). The

main drawback, however, is that an increase in k will make this test very conservative, the chances of Type II error increases. Thus, I used this test only when $k< 10$.

When using a parametric ANOVA I decided to use the Least Significant Difference test (LSD), but only after checking for the homogeneity of variance among the samples through a Levene's test. The greatest advantage of the LSD test is its consistency, i.e. it can point to differences amongst means independent of the range of means (Saville, 1991; Zar, 1996). When the variances differed significantly, I used the Games-Howell *post hoc* test, which among the available options (Tamhane's T2, Dunnett's C and Dunnet's T3) provides the most accurate results, even when sample sizes are unequal (Field, 2000).

All tests are two-tailed, unless otherwise stated, and a value of p=0.05 was used throughout.

Sampling methods

The detailed methods used for sampling vegetation and phenology, insect abundance and mammal densities are presented in Chapters III and IV. In Chapter V I give the details of all behavioural observations made on the capuchin monkeys to assess their foraging and feeding strategy and further details on sampling abundance and diversity of insect resources used by the monkeys. In Chapter VI the observations of tool use in feeding and methods of analyses are presented. Definitions of all behaviour are given in relevant chapters and the total hours of observation and sampling are presented in Appendix 6.

Trees on the Jurubeba trail during the dry season

Chapter III

DIVERSITY, STRUCTURE AND FOREST PHENOLOGY

INTRODUCTION

"If the traveller notices a particular species and wishes to find more like it, he may turn his eyes in vain in any direction. Trees of varied forms, dimensions and colours are around him, but he rarely sees any of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct. He may at length, perhaps meet with a second specimen half a mile off, or may fail altogether, till on another occasion he stumbles on one by accident" (A. R. Wallace, 1876, quoted in Hurlbert, 1971). Indeed, no description could be such a perfect antithesis of the Caatinga dry forest. The Caatinga is a sea of sameness, here and there a different tree species is found, but invariably some particularity of the terrain (sandy or clay soil, availability of water, etc) and history of disturbance will explain its appearance. How does this low diversity and apparent homogeneity affect the vertebrate community?

Dry forests normally have a much lower diversity and a low net primary productivity than rainforests (Murphy and Lugo, 1986) and periods of fruit scarcity are much longer than in tropical rainforest (van Schaik *et al.*, 1993). These features apparently have an effect on vertebrate community that tend to be characterized by a lower number of species and low abundance, and the Caatinga has one of the lowest diversity of vertebrates among Neotropical dry forests (Ceballos, 1995). The mammalian fauna, in particular, is considered one of the poorest faunas in the tropics and has the lowest density of small terrestrial mammals among the tropical arid and semi-arid environments (Mares *et al.*, 1985). Fruit-eating specialists seem to be particularly scarce, probably because of the highly seasonal and often unpredictable

availability of fruit (Machado *et al.* 1997), but low number of tree species producing fruits could account for this. For instance, in most Neotropical forest about 69% of tree species produce edible fruit for vertebrates (Gentry, 1982), while in the Caatinga an estimated 26-40% of the flora have zoochoric fruit that rely on animals for seed dispersal (Machado *et al.,* 1997; Griz and Machado, 2001; Tabarelli *et al.* 2003). Is the impoverished mammalian community of Caatinga reflecting low diversity of trees or is it a consequence of human disturbance (Chapter II)?

In this chapter I will provide a detailed description of the vegetation, differences in diversity and phenology of trees occurring in different habitats and make some inferences on how these factors can affect the vertebrate community. The Caatinga seems to be a relatively homogeneous forest, but to what extent? Furthermore its homogeneity in structure mask an enormous diversity through time, when resources are briefly abundant only to vanish in the dry season.

Aims

1- Evaluate the plant communities in different types of habitat by comparing forest structure, species richness and floristic composition;

2- If there are differences in plant communities between habitats what are their origins (human disturbance; ecological factors and type of soils) and how are these differences reflected in the fruit production (with direct implication for abundance and distribution of different animals) and phenology of trees?

3- And finally to compare species richness and abundance of the Caatinga dry forest with other dry forest and find out how much the Caatinga can be similar or different in relation to other Neotropical dry forests.

METHODS

Habitats and areas sampled

For the vegetation analyses I sampled three main habitats in the area where this study was carried out, namely Cliffs, Canyons and Plateau (Chapter II). Each of these habitats has a particular type of vegetation as outline in Chapter II. For evaluating the differences among these habitats I used vegetation transects placed in 6 locations widely spread over the park (see Fig. 3 in Chapter II). The sampling effort was slightly more intense in the home range area of the focal capuchin monkeys group (Chapter V) and also in the Canyon habitat, since I expected this habitat to be more heavily used by the monkeys and other mammals due to its relatively lush and wetter condition when compared to the surrounding areas.

Sampling tree abundance and distribution

To determine the diversity, abundance and distribution of trees, I used belt transects based on the standardised sampling protocol for vegetation suggested by Gentry (1982; 1988). He recommended the use of 10 plots measuring 50 x 2m (totalling 0.1 ha) located randomly in the area to be sampled and all of the plants with a diameter at breast height (DBH) $\geq$ 2.5 cm and rooted within the belt transect are measured (height and diameter) and identified. On a local scale, narrow transects sample greater habitat variation and associated changes in species composition, and thus perform better in habitats with higher heterogeneity than the frequently used square plots (see Krebs, 1999). Despite the relatively small area sampled, Gentry (1982) showed convincingly that his sampling protocol is adequate for analyses of tropical forest communities. Indeed, this method is more efficient, in terms of number

of trees and species sampled, when compared to the 1 ha plot size methodology routinely and extensively used by botanists across the Neotropics (Phillips *et al.*, 2003). The efficiency of Gentry's sampling protocol could be even higher in dry forests, which are simpler in structure and plant diversity in relation to the wet forests. Furthermore, this method has been used in different types of dry forest (e.g. Gillespie, 1999; Gillespie and Jaffre, 2003; Sussman and Rakotozafy, 1994; Trejo and Dirzo, 2002; Varela *et al.,* 2002), hence possible biases associated with different methodologies are reduced during comparisons.

Nevertheless, Rosenzweig (1995) has criticised the use of this method, since a small plot size could lead to spurious comparisons of diversity between different areas. He showed that plot sizes of 0.1 ha are not larger enough for evaluating plant diversity and usually do not give an adequate reflection of the diversity of larger areas, thus in some cases leading to erroneous assumptions about diversity when comparing species-area curves. He estimated that tree and shrub diversity could be adequately studied in a sample area of about one hectare. Therefore, I decided to use a modified sample protocol and to increase the area sampled in the different habitats.

In the modified sampling protocol, I used rectangular quadrats measuring 250 x 4m divided in sub-plots of 50 x 4 m. These belt transects sampled a minimum area of 0.1 ha and a maximum of 0.5 ha (Table 1). Most of these belt transects were located along the trails used for mammal censuses (Chapter IV). In trails longer than 1km, I divided the trail at intervals of 250 m and then randomly selected a start point for each of the belt transects. By tossing a coin, I chose which side of the trail the quadrat was placed. If the chosen side had a rock outcrop formation I changed sides and if both sides had rock outcrop formations, I kept to the transect and sampled any trees within it.

Table 1. Details of the vegetation transect established in different habitat types in the Park.

Place	Habitat type	Sampling type	Total sampled area (ha)
Baixa Grande	Cliff	Belt transect	0.4
Oitenta, B. Grande and Jurubeba	Cliff	Square plots	0.5
Esperanca	Canyon	Belt transect	0.5
Baixao da Vaca	Canyon	Belt transect	0.5
Boqueirao da Beti	Canyon	Belt transect	0.1
Oitenta Canyon	Canyon	Belt transect	0.1
Caldeirao do Gato	Canyon	Belt transect	0.1
Zabele	Plateau	Belt transect	0.3

Along the Cliffs the vegetation seemed to present a greater variability, probably due both to human disturbance and heterogeneity of habitats (the topography was more rugged). Hence, there was a possibility that the belt transect would not truly sample all the variability. To circumvent this likely bias in sampling, I delimited eight plots measuring 25 x 25m distributed in an area of about 400 ha. The distance between these plots ranged from 70m to about 5km and they were located at varying distances from the Cliffs; the closest being about 10m and the furthest circa 800m (see Fig. 3, Chapter II).

Inside the transects and plots, all trees with a girth of $\geq$ 12cm circumference (diameter $\geq$ 3.8cm) were measured and the height estimated. The trunks were numbered with indelible ink pencil for further analyses of phenology. The DBH used was larger than that suggested by Gentry (1982), because the majority of floristics studies in the Brazilian dry forest use DBH $\geq$ 3 cm (e.g. Araujo *et al.*, 1995; Lemos and Rodal, 2002; Ribeiro and Tabarelli, 2002). When I found trees with multiple stems I took the measure of all stems within the stipulated DBH, but for analyses I

used only the largest stem following Cadotte *et al.* (2002) and Condit *et al.* (1996). Lianas were not sampled, because in some points along the Cliffs and in some of the Canyons (Baixao da Vaca and Boqueirao da Beti) they were cut as a management strategy by the park direction in order to improve tree growth and avoid their death. I sampled a total area of 2.5 ha distributed in different habitats as noted in Table 1.

Tree phenology

All of the trees in the belt transects and plots were monitored once a month for the presence of leaves, flowers, fruit, leaf fall and leaf flush. Leaf fall was based on the presence of bare branches on the tree, dead leaves on the ground and the characteristic 'autumn' colour of leaves. Phenological data were collected from June 2001 to January 2002 for a total of 8 months, covering four months of the rainy season and four of the dry season. Whenever possible I took additional *ad libitum* observations on the presence of fruits that could be eaten by the monkeys or other vertebrates. A phenological study should ideally last at least one year (sampling two different wet seasons) and phenological data collected biweekly, since some tree species in the Caatinga present massive flowering after the first rain and the flowers last between less than one week to two week (e.g. *Ptilochaeta* sp. and *Calliandra* spp.). Unfortunately, there were a series of logistical constraints that preclude more than two phenological observations/month, e.g. it was extremely hard and time consuming to open and demarcate some of the belt transects, I obtained field assistants only from April 2001 and even so for only 3 months. Nevertheless, the random sampling of phenological patterns, i.e. the interval between observations varied from 1.5 weeks to almost four weeks; and the fact that most of trees whose are

dispersed by vertebrates produce fruit during the rainy season (Machado *et al.*, 1997), suggest that the results I obtained could be extrapolated to a full year.

Monitoring the tree phenology in the Plateau was more problematic than other areas. For example, the fading of the 'indelible' ink from the tree tags, as a result of exposure to sun, meant that many individuals were lost and considerable effort was required to re-tag all of the trees or most of them on a monthly basis. Moreover, the higher density of trees in the Plateau (see below) and a lack of field assistants for most of the study duration lead to a greater amount of time spend in monitoring the phenology of trees. On some occasions I just could not allocate time from other activities for monitoring the trees in the Plateau habitat.

Analyses of data

I used one-way ANOVA to compare forest height within and among the habitats and also for comparisons of species diversity (Chapter II). When the assumptions of normality and homogeneity of variance were not met I used the Kruskal-Wallis non-parametric ANOVA.

One almost obligatory parameter used for representing ecological dominance by a tree species, genus or family and making comparisons between different areas is the basal area (e.g. Cadotte *et al.,* 2002; Ferreira and Prance, 1998; Milliken, 1998). However, too much value may have been placed on basal area as an indicator of importance or dominance, as it can lead to dubious comparisons. For instance, a single tree species with a larger DBH would rank higher than another species with 10 or more individuals, but with a lower total DBH. Moreover, life history traits can also induce misleading comparisons using basal area alone, since some species such as *Cavanillesia* spp. have a barrel-shaped trunk used for water storage, others like

Enterolobium spp. develop large trunks for their size, while other species common throughout the Caatinga dry forest, such as *Croton* spp., *Mimosa* spp., *Capparis flexuosa* and others hardly grow in girth. Thus, the use of density or relative proportion is a more sensible approach for comparing different habitats and for inferring the importance of a given species or tree family for a particular area.

There was no variability in DBH and height of trees between the square plots and the belt transect along the Cliffs (Levene's test for equality of variances $F=2.5$, $p= 0.11$ and $F= 0.052$, $p=0.82$, $df= 871$). Similarly, the species diversity in the plots and the belt transect did not differ (Shannon index, $H'= 2.7$ and 2.68; $t= -0.058$, $p= 0.56$). Thus, I combined both samples as Cliffs and carried out all the comparative analyses based on the combined variables' value, unless otherwise specified. The Canyons B. Beti, Oitenta Canyon and C. Gato (Table 1) were relatively close to each other (Fig. 3 in Chapter II), with a similar length (range 400-800m) and within or around the home range of the focal capuchin group. Thus, I combined them as Canyons I and carried out the analyses on this combination. The Baixao da Vaca and Esperanca Canyons had similar sizes (1.3 km and about 2.3 km respectively), a similar floristic composition and were closer to each other thus they were combined as Canyons II.

In order to analyse the abundance of trees producing fruits used as food resources by the vertebrates in the different habitats, I grouped the trees into classes of seed dispersal based on fruit type and species life history traits from the literature (e.g. Machado *et al.*, 1997; Griz and Machado, 2001). If I could neither observe the fruit nor identify the tree, I considered the dispersal type as unknown. Yet, some species such as *Enterolobium* cf *contortisiliiqum*, *Caesalpinia ferrea* and *Chloroleucon* cf *dumosum* had fruit (pods) that seemed to be dispersed by vertebrates, but I could not find any confirmation and thus I label their dispersal type as unknown.

Habitat heterogeneity and species variability

Habitat heterogeneity is an important factor accounting for differences in species diversity and is frequently associated with β-diversity or the change in species composition across space (Whittaker, 1972). To assess the variability of species richness within the habitats sampled, I used the coefficient of similarity of Jaccard (Krebs, 1999):

$$J = \frac{a}{a + b + c}$$

Where: a= # of shared species between plots 1 and 2; b= # of species exclusive to plot 1; c= # of species exclusive to plot 2.

The value of J varies from 0 (no similarity) to 1 (complete similarity), and this is a commonly used index for evaluating β-diversity among different areas (e.g. Balvanera *et al.*, 2002; Condit *et al.,* 2002; Cadotte *et al.*, 2002; Magurran, 1988). For each comparison within habitats I used the 0.1 ha plots and calculated the coefficient of similarity for all possible combinations of the 0.1 ha plots in a given habitat type.

Species diversity and identification

I used two measure of species diversity: Fisher's α and Shannon index of diversity (H'), both widely used in floristic studies. Details about these methods were given in Chapter II.

Most of the trees were identified in the field, and specimens from most were collected and are deposited at the Herbarium JPA, University Federal da Paraiba. Where the species could not be identified botanically but could be clearly distinguished on general grounds, these unidentified were named "Unknown sp.1" and so on.

RESULTS

Forest structure, composition and level of disturbance in the different habitats

Across the different habitats sampled a total of 2786 trees were identified and 2746 were measured[1]. The forest in these habitats was very variable in terms of physiognomy (tree height and density) and species composition. The Canyons had a taller forest with trees up to 25 m and with larger diameters than other habitats. The Sapotaceae and Sapindaceae attained their highest density in this habitat (Table 2). In all the habitats but Canyons I, the Leguminosae *lato sensu* was the family with the highest density. The Cliffs were relatively similar to the Canyon II in terms of tree density and height, but in the Cliff forest the dominance of Bignoniaceae and Combretaceae was striking. Accordingly, the Cliffs forest was dominated by 3 species: *Tabebuia impetiginosa* (22.4%, Bignoniaceae), *Thiloa glaucocarpa* (15.5%, Combretaceae) and *Anadenanthera colubrina* (11.2%, Leg., Mimosaceae), which together make up over 49% (n= 873) of all trees in this habitat. The reasons for the preponderance of these species in the Cliffs habitat are unknown. However, all of them are wind dispersed and *T. glaucocarpa* apparently is a common species in middle stage of Caatinga forest succession, these features probably explain their success in this habitat and can be associated with past human disturbance. Indeed, along the Cliffs the rocks showed an indelible signal of rampant fire in the past, the

[1] The number of trees measured was lower because during the measurements in the Plateau, the trees in one of the sub-plots (50 x 4m) were assumed to have been measured, but were not. When I found out, it was too late to re-measure.

Table 2. Gross characterisation of forest structure and tree density across the different places sampled. Lau= Lauraceae; Leg= Leguminosae; Bign= Bignoniaceae; Com= Combretaceae; Lau= Lauraceae; Myrt= Myrtaceae; Ery= Erythroxilaceae; Sapin= Sapindaceae; Sapot= Sapotaceae; Nyct= Nyctaginaceae.

Place	Area Sampled (ha)	Number of trees	Trees/ha	Maximum tree height (m)	Maximum tree DBH (cm)	Families with highest number of individuals
Canyons I	0.3	440	1,466	25	75.8	Myrt(195); Ery(55); Lau(28)
Canyons II	1	981	981	22	105.4	Leg (263); Sapin(163);Sapot(131)
Cliffs	0.9	873	970	20	83.12	Leg (272); Bign(200); Com(135)
Plateaux	0.3	492	1,640	7	31.8	Leg (326); Myrt(82); Nyct(24)

vast majority of rocks exhibited carbon or soot. These fires were probably set to clear the land for agricultural activities and were common until the recent past (see Chapter II) and, as a consequence, the forest along the Cliffs was a mosaic of different stages of recovery. Nonetheless, the heterogeneity of the terrain was also an important aspect accounting for the composition and structure of the forest.

The Canyons I and II had marked differences in terms of forest structure (see below) and composition (Table 2). In Canyons I, the commonest species were *Eugenia* sp (Myrtaceae), accounting for 33% of all trees (n=440) followed by *Erythroxylum* sp.1 (12.6%, Erythroxylaceae) and *Ocotea* sp.1 (5.9%, Lauraceae), while in the Canyons II *Senna spectabilis* (Leg., Ceasalpiniaceae) and *Talisia esculenta* (Sapindaceae) were the most common species (15.2% and 13.3%, n=981) followed by *Pouteria* sp.2 (10.5%). The preponderance of *S. spectabilis* in Canyons II was a result of disturbance. This species was dominant in areas recovering from past agricultural activities. Canyons II seemed to have experienced more disturbance than Canyons I, but it would be wrong to assume that the forest in Canyons I were pristine. The Canyons I had a relatively short length compared to Canyons II and past agricultural activities inside seemed to be non-existent, probably due to a low return of crops planted in a small area. I found evidence that the forest had been selectively logged in Canyons I, albeit in a light way.

Finally, the Plateau had a short deciduous forest, with a maximum tree height of 7 metres (just one tree), with a relatively dense understorey, and a larger number of lianas. In this habitat the Leguminosae attained the highest density amongst the sampled habitats (Table 2) The forest on the Plateau had a peculiar physiognomy mainly produced by the most common species there; *Cassia eitenorum* (16.7%, n= 492) with its shiny leaves, *Pterodon abruptus* (11.8%) with its widely spreading

branches and *Cenostigma gardneriana* (10.8%) with an striking and unmistakable engraved trunk.

Interesting, the Canyons and Cliffs had a relatively open forest (a lower density of trees), while in the Plateau the forest was more 'packed' (Table 2). Over all habitats I found a density of 1114 trees/ha.

The variation in the height of trees among the different habitats sampled was considerable (Fig. 6). In general, trees inside the Canyons and along the Cliffs were significantly taller than in the Plateau habitat (ANOVA, $F_{3,\ 2745}$= 330.1; Games-Howell *post hoc* test, p<<0.001), but the trees in both Canyons habitat differed in height. Trees in Canyons I attained significantly higher height than in Canyons II (Games-Howell *post hoc* test, p<<0.001). The height of trees in the Cliffs was similar to the Canyons II (Games-Howell *pos hoc* test, p= 0.2). Trees, above 10 m, represented only 8.5% of all the trees sampled and over 4% of these are located inside the Canyons. Actually, there is a large contrast between the proportion of lower and "upper" layer species among the different vegetation sampled.

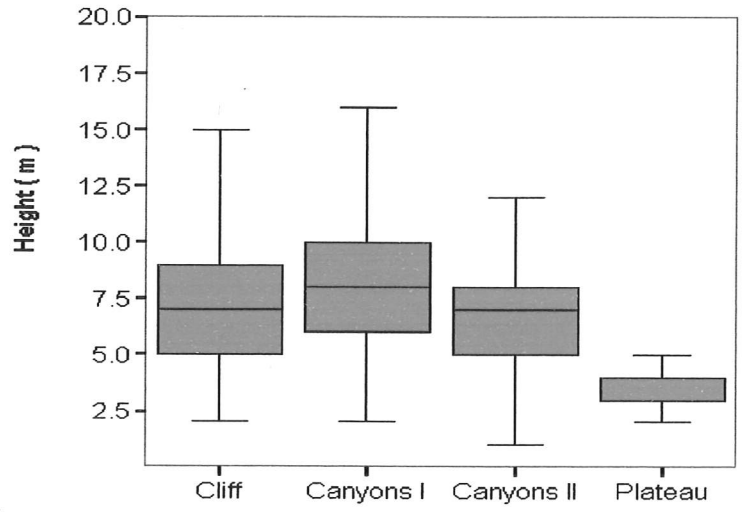

Figure 6. Variability in the height of the trees among the different habitats. Boxes show upper and lower quartile and lines represent the lowest and highest observed values.

Assigning height classes to the forest could be misleading, since it could create 'artificial' layers and this is particularly true in places where the forest is recovering from disturbance. Nonetheless, I could identify three main strata based on some common species that had attained full growth. For instance, along the Cliffs a lower strata (1-3 m) could be delimited by *Capparis flexuosa* (average height= 3 m ± 1.18 SD, mode = 2 m, n= 16). *Ruellia* spp (Acanthaceae) and *Alternanthera* sp. (Amaranthaceae) were very common in this strata, but they had too small a DBH (<2.5 cm) to be included in the sampling. *Bauhinia cheilanta* ($\bar{x}$= 5.4 m; ± 1.4 SD; mode=6; n= 30) and *Croton sonderianus* ($\bar{x}$ = 5.5 m; ± 1.2; mode=6; n= 50) and other less frequent species formed a middle storey (4-6m) in the forest along the Cliffs. Inside the Canyons, a 'true' understorey (1-3 m) was almost absent, I could observe only some unidentified small Euphorbiaceae trees (about 1.5 m) but with a small DBH. However, the presence of a middle stratum composed mainly by *Erythroxylum* sp.1 = 6.82 m; ± 2.2 SD; mode=6; n= 64) and *Cybianthus* sp. ($\bar{x}$ = 5.62 m; ± 0.91 SD; mode=6; n= 8) was clearly visible. Altogether, the height classes I used for the different forest strata fit relatively well into the observed strata in the forest occurring in the different habitats.

Overall, the forest layers were relatively simple in the Plateau, where just two distinct layers could be found. The forest structure was more complex in the forests along the Cliffs and inside the Canyons (Fig. 7). Along the Cliffs most of the canopy overstore (7-10 m) was formed by *A. colubrina* and *T. impetiginosa* and in the Canyons this strata was formed basically by *Eugenia* sp., *Ocotea* spp. and *Pouteria* spp.

Although Murphy and Lugo (1986) considered that most of the dry forest had just one or two canopy strata, in my study site I found up to 4 different forest strata, except in the simpler Plateau forest. Despite the previous caveat that the forest in many places is still recovering and growing after human disturbance, the structural layers that I show here seem to reflect a natural stratification in this particular Caatinga forest.

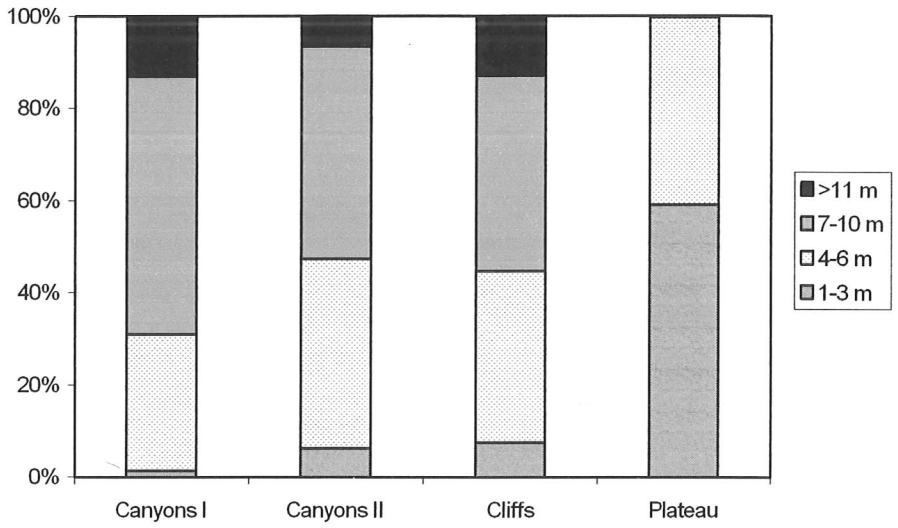

Figure 7. Structural layers of the forest in the different habitats sampled using height classes

The DBH of trees in the different habitats differed significantly (Kruskal-Wallis H= 80.9; df= 2; $p<<0.001$). Yet, the Canyons II and Cliffs were very similar in average DBH, while the trees in the Plateau had significantly smaller DBH and the trees in Canyon attained a significantly larger DBH than did trees in the other habitats (Mann-Whitney test, $p< 0.001$, Bonferroni correction) (Fig. 8).

Trees with DBH $\geq$ 10 cm were more frequent in the Canyons (I and II, 39.1%, n= 1421) and along the Cliffs (33.5%, n= 873). The Plateau exhibited a low proportion of trees with DBH $\geq$ 10 cm (Fig. 9). The tree with the largest trunk was

located inside the Canyons II, *Inga* aff. *capitata,* with a diameter of 105.4 cm. Other trees inside the Canyons also with larger trunks were *Brosimum* cf. *alicastrum* (DBH= 62.7 cm), *Ocotea* sp.1 (DBH= 50.6 cm) and an unidentified Sapotaceae (DBH= 75.7 cm). Along the Cliffs, the largest trunk was from a *Ficus gomellera* (DBH= 83 cm). In the Plateau the largest trunk diameter recorded were from *C. gardineriana* (DBH= 31.8 cm) and *P. abruptus* (28 cm).

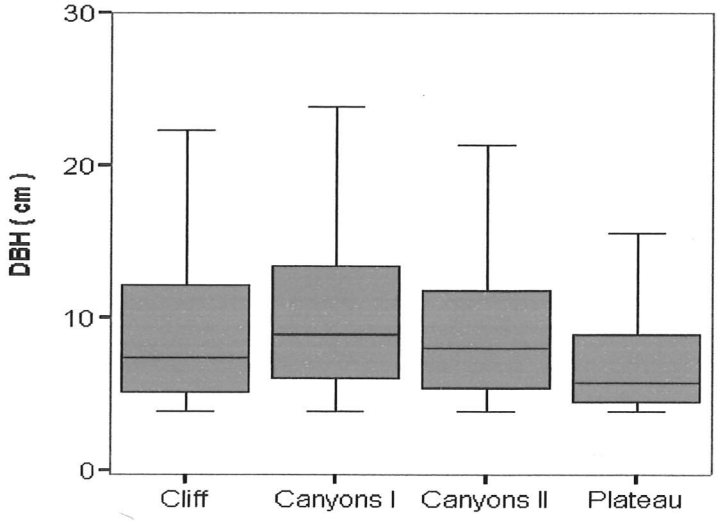

Figure 8. Variation in the diameter at breast height (DBH) of trees in the different habitats sampled. Boxes show upper and lower quartile and lines represent the lowest and highest observed values.

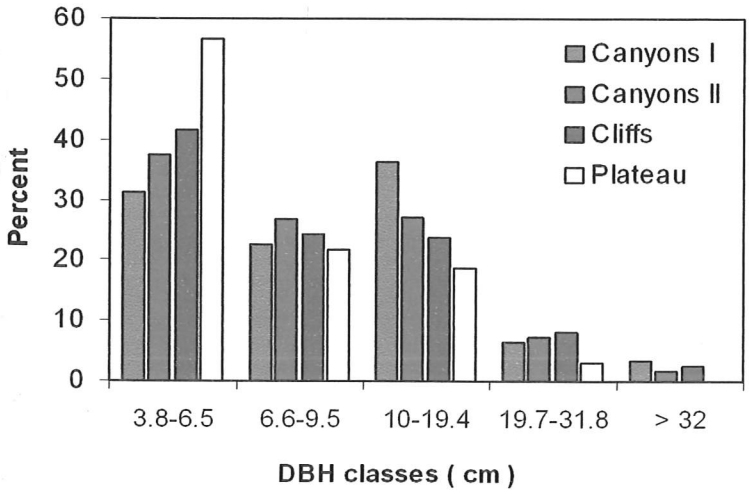

Figure 9. Proportion of trees in the different DBH classes per habitat sampled.

Within each habitat type the variability in DBH was strikingly high (Fig. 10). The Plateau, however, exhibited a more homogenous forest and the lower variability in DBH could be seen as an indication either of a more pristine condition or a greater simplicity in structure and life history traits of the species occurring there.

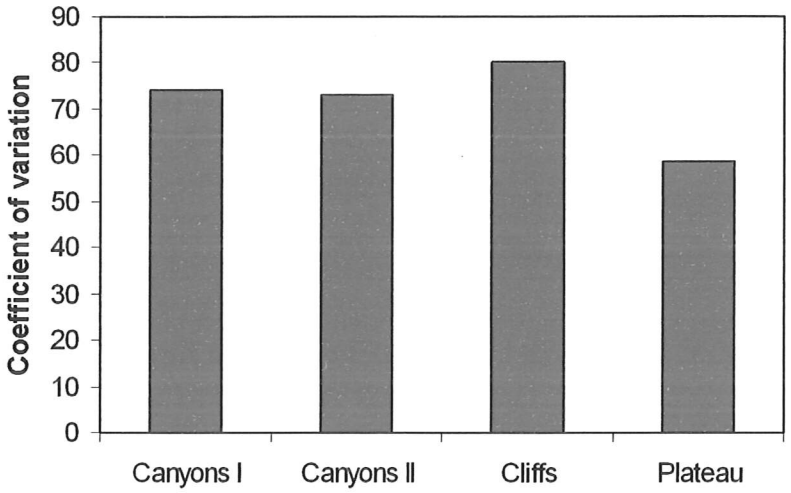

Figure 10. Within habitat Coefficient of Variation in DBH.

Dispersal types

Most species of trees (52.1%, n=121) were dispersed by vertebrates, but among the different habitats there is a significant difference in the proportion of zoochoric trees (Fig. 11). The Cliff habitat had the lowest number of trees dispersed by vertebrates, while the Canyons had the highest number, indicating that in this habitat there is an important interaction with the frugivorous vertebrate community.

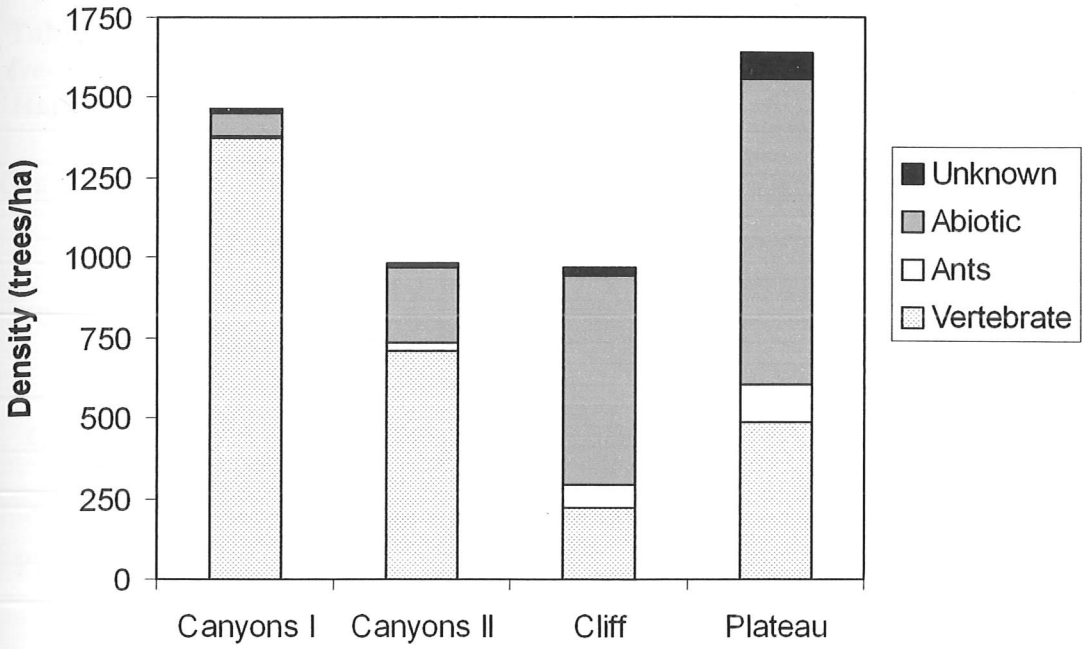

Figure 11. Dispersal types and tree density at different areas sampled. Unknown dispersal was scored when the plant could not be identified and fruits were not observed.

This difference is even more apparent when looking at the density of the three most frequent species dispersed by vertebrates (Table 3). The Cliffs pale in comparison with the other habitats. Interestingly, the different habitats differ markedly in the number of zoochoric species (χ^2= 14.3; df= 3; p= 0.02), but this difference is due only to the Plateau (Table 3). The Canyons I and II had similar number of zoochoric species (38 and 34 spp. respectively) and the number of zoochoric species in the Cliffs was significantly higher than in the Plateau habitat (χ^2 = 5.1; df=1; p= 0.023).

Table 3. Details of zoochoric species found in the different habitats and the most frequently observed in each habitat.

Habitat	Total number of zoochoric species	Species	Density (trees/ha)
Canyons I	38	*Eugenia* sp.1.	483.3
		Erythroxylum sp. 1	183.3
		Ocotea sp.1	86.7
Canyons II	34	*Talisia esculenta*	130
		Pouteria sp. 2	103
		Ocotea sp.1	81
Cliffs	26	*Talisia esculenta*	37.8
		Prockia crucis	25.5
		cf. *Eugenia* sp.	24.4
Plateau	12	Myrtaceae Unknown sp. 2	113.3
		cf. *Eugenia* sp.	80
		Guapira sp.	80

Species diversity

Habitat heterogeneity and beta diversity

The differences between habitats in relation to which family was commoner and the differences in density of some particular tree species (see above) hints at a high β-diversity. Indeed, the similarity among 0.1 ha plots in the different habitats was complex and they tended to show a low index of similarity (Fig. 12), indicating a higher turnover of species (high β-diversity). One would expect that the more distant the plots are, the higher will be the change in species composition. A parametric correlation between distance (using the 25 x 25 m plots) and the Jaccard index, revealed no relationship ($r= 0.07$; $n= 28$; $p=0.7$), but close proximity was not a main factor linking the 0.1 plots. For instance, Caldeirao do Gato more similar to plots of Baixao da Vaca and Esperanca and yet it was closer in space to Oitenta Canyon and B. Beti, while others such as the cluster (Aep(Abv(Bbv(Cbv)))) seemed to be grouped

by their similar level of disturbance and associated vegetation rather than proximity. Nevertheless, all these plots grouped clearly into the three main habitats sampled.

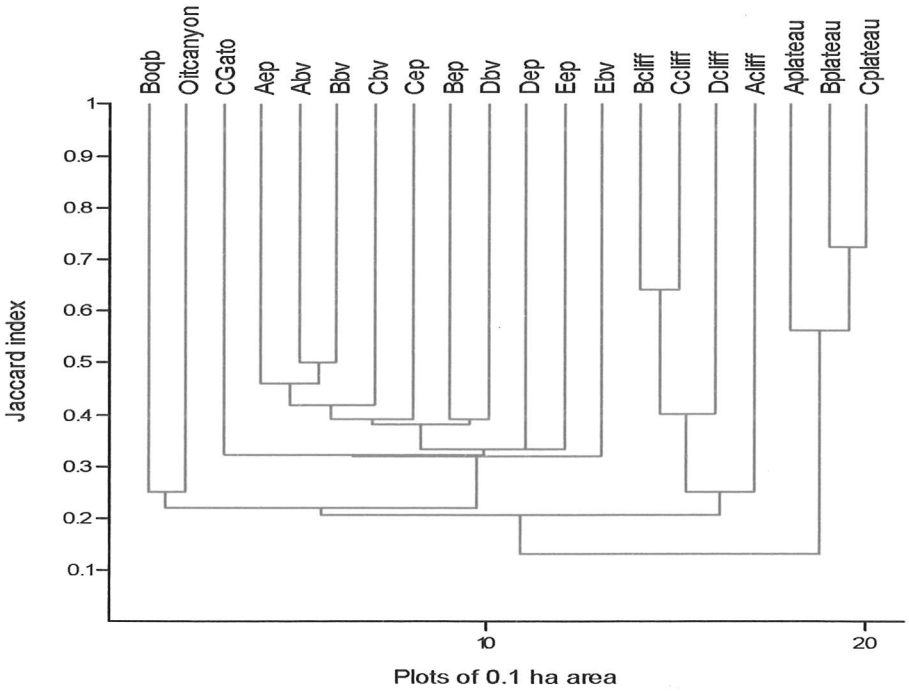

Figure 12. Level of similarity between plots of 0.1 ha in the sampled habitats. Boqb= Boqueirao da Beti; Oitcanyon= Oitenta Canyon; Cgato= Caldeirao do Gato; ep= Esperanca Canyon; bv= Baixao da Vaca Canyon. The alpha code goes from the beginning to the end of the transects. The clusters were linked using the Single linkage method (see Krebs, 1999).

The differences in level of similarity among the different plots were not unexpected, since the habitats presented marked differences related to soil depth, soil structure and water availability, e.g. the Canyons are wetter, and Cliffs have a greater physical heterogeneity. Interestingly, a comparison of the similarity index between the Canyons (I and II) and the Cliffs revealed that they share 26.2% of the tree species, while for the Plateau x Canyons and Cliffs it resulted in just 3.3% of shared tree

species. The forest on the Plateau was very peculiar from a floristic point of view, with unique species and apparently with a limited distribution in the Caatinga biome.

The Cliffs presented the most heterogeneous habitat, with a very rocky soil and greater variability in the availability of water, due both to differential shade (by big rocks and the Cliffs) and underground water accumulation. As such, I expected the greatest variability in species turnover in this habitat, but when I analysed the variability of species composition among the plots in the different habitats it was the Canyons that had lower similarity between their plots (Fig. 13). The average similarity between trees species among plots within habitats was just 29% in the Canyons (I and II) and slightly higher in the Cliffs (35%), while the Plateau was more homogenous with up to 60% of similarity in species composition among its plots, revealing that species turnover was higher in the Canyons. The greater difference in species composition among plots in the Canyons probably is a consequence of human disturbance. In the largest Canyon, Esperanca, agricultural activities were common in some areas close to its entrance until 10 years ago. The first and second 0.1 ha plot in this Canyon had vegetation that was in process of recovering from disturbance. The Baixao da Vaca Canyon had a much more disturbed vegetation than did Esperanca; it was inhabited by one family before the creation of the Park. Only in its terminal area was the vegetation less altered.

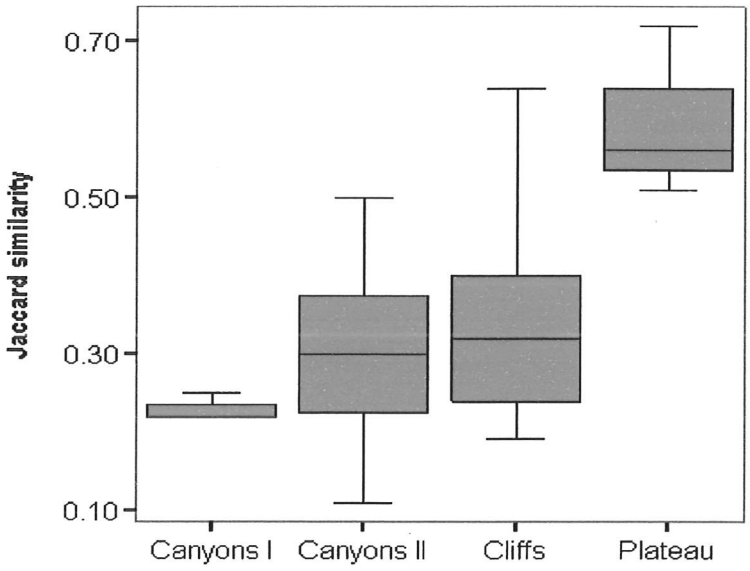

Figure 13. Similarity in floristic composition within 0.1 ha plots in the different habitats. The lower the similarity, the higher the β-diversity.

Difference between habitats

The 2786 trees sampled over 2.5 ha contained 121 species distributed in 71 genera and 38 families (Appendix 1). The most important family in the area, in terms of density and number of species was Leguminosae *latu senso,* and the different habitats showed a clear variability in the number of species.

The simplest way to portray diversity is just the number of species observed, however, increasing the sampled area will inevitably raise the number of species. The cumulative species-area curve indicates that among the habitats only the Cliffs and Canyons II were reaching an asymptote (Fig. 14a.), it also reveals the Plateau as the habitat with higher number of species per sampled area. With an area of 0.16 ha about 88.5% and 63.1% of the species were sampled in the Plateau and Canyons I, and probably the species-area curve was closer to reaching an asymptote. The overall

cumulative number of species in 1.5 ha represented 80% of all tree species and at around 2 ha, the species area-curve reached an asymptote, rising only very slowly as increasingly rare 'new' species were added (Fig. 14b.).

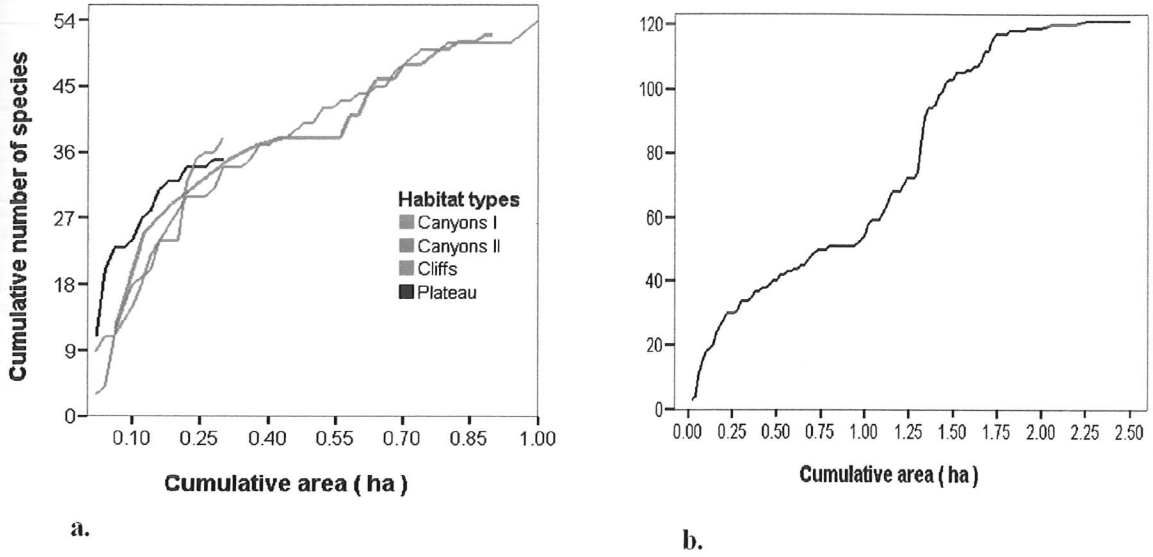

Figure 14. Cumulative species-area curve for the different habitat sampled (a.) and for the total sampled area (b.).

Considering the total number of sampled trees in the different habitats, the Canyons II and Cliffs presented the highest diversity accordingly to the Shannon index (H') and Fisher's α (Table 4). Yet this result could be just an artefact of the small sampled area in the Plateau and Canyons I. Moreover, although the Fisher's α diversity index is considered independent of sample size (Chapter II), it tends to exhibit a higher standard error with small sample sizes (Fisher *et al.*, 1943). Nonetheless, the Plateau did have the highest diversity. It is possible that more than one species was grouped as 'lost' (due to the fading of ink on the tags) and more species did not attained the minimum DBH in the Plateau than in any other habitat

sampled. Perhaps the best way to deal with these discrepancies is to compare the average diversity across plots of identical sizes. Thus, I calculated the species diversity per 0.1 ha plots and analysed the differences between the habitats again on that basis.

Table 4. Overall species diversity in the different habitats.

Diversity	Canyons I	Canyons II	Cliffs	Plateau
# trees	440	981	873	492
# species	38	54	52	35
H' (Shannon)	2.608	3.093	2.902	2.885
α (Fisher)	9.976	12.3	12.12	8.616

Species richness in 0.1 ha plots ranged from 11 to 27 species with an average of 18.3 species ± 5.03 SD and a mode= 13 species per 0.1 ha plots. The Plateau presented remarkable evidence of being the habitat with the highest diversity of trees. All of the different measures of diversity, i.e. # species observed, Shannon index and Fisher's α, were much higher in the Plateau (Fig. 15). An ANOVA, based on the variability of the Shannon diversity index per 0.1 ha plots, indicated that there was a strong, albeit not significant, difference in species diversity among the different habitats ($F_{3, 16} = 2.59$; $p=0.08$). This trend toward significance was mainly due to the higher diversity in the Plateau in relation to the Canyons I and II (LSD post-hoc test, $p= 0.046$ and $p= 0.017$ respectively), while the Cliffs presented diversity similar to the Plateau[2].

[2] A small sample size makes a statistical test more conservative. Using species richness in 0.02 ha plots, increasing the sample size, the differences turn highly significant ($F_{3, 96}= 13.1$; $p<<0.01$) and the Plateau is the only habitat to differ significantly in diversity (Games-Howell *post hoc* test, $p<0.001$) from all the other habitats.

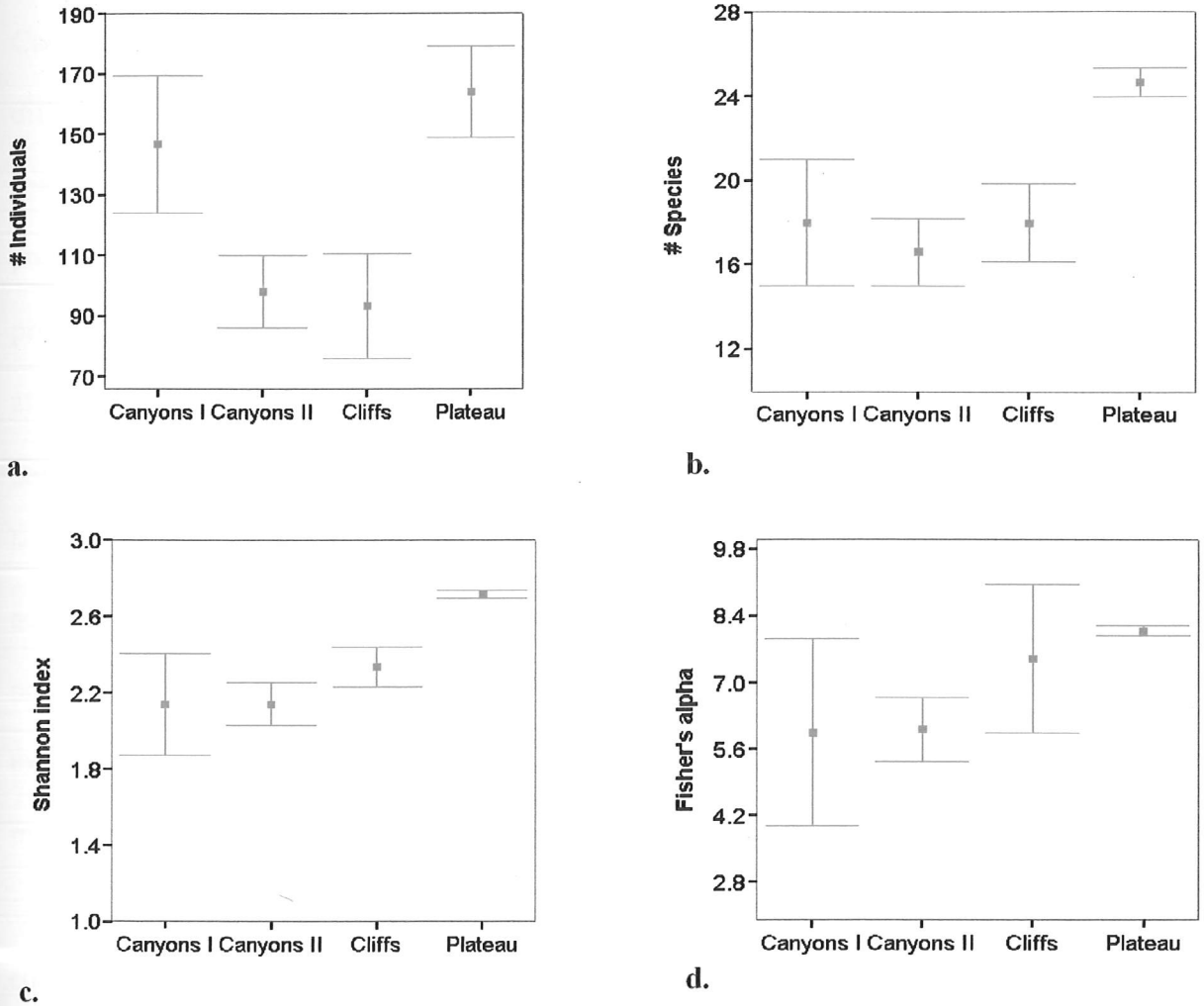

Figure 15. Indices of species diversity in the different habitats sampled. The values were calculated as average for 0.1 ha plots. The bars indicate one standard error.

Phenology in the forest

Differences between habitats

In the more deciduous areas the leaf fall usually started in May and reached a peak in June-July. Leaf fall was associated with dry conditions generally, either due to low rainfall or low water table levels, but there was a considerable contrast in

the phenology of the forest occupying the different habitats (Fig. 16). Although the Canyons I and II were almost identical in the proportion of leafless trees, they did differ significantly in the proportion of trees that kept leaves throughout the dry season (Kolmogorov-Smirnov two sample test, $Z= 1.75$; $n= 8$; $p<0.01$) and in the proportion of fruiting trees ($Z= 1.75$; $n= 8$; $p<0.01$) (Fig. 12a. and c.). The high proportion of leafless trees in Canyons II during the dry season (May-Oct.) can be attributed to the vegetation in the recovering areas. Most trees species there, such as *Senna spectabilis, Mimosa acutistipula, M. tenuiflora* and *Croton sonderianus*, were leafless in the dry season. The degree of deciduousness, nevertheless, varied according to the habitat type. Interestingly the Canyons II and Cliffs had a similar proportion of trees bearing fruits (Kolmogorov-Smirnov, $Z= 0.5$; $n= 8$; $p=0.9$) and most of them fruited in the dry season (Fig. 16d), but these trees were composed mainly of species with abiotic (mostly wind) dispersal types (see below).

The overall proportion of trees flowering and fruiting was lower, probably a consequence of a drier year when these data were gathered. Many species failed to produce flowers, for instance *Tabebuia impetiginosa* is the commonest species along the Cliff habitat and just a single individual produced flowers.

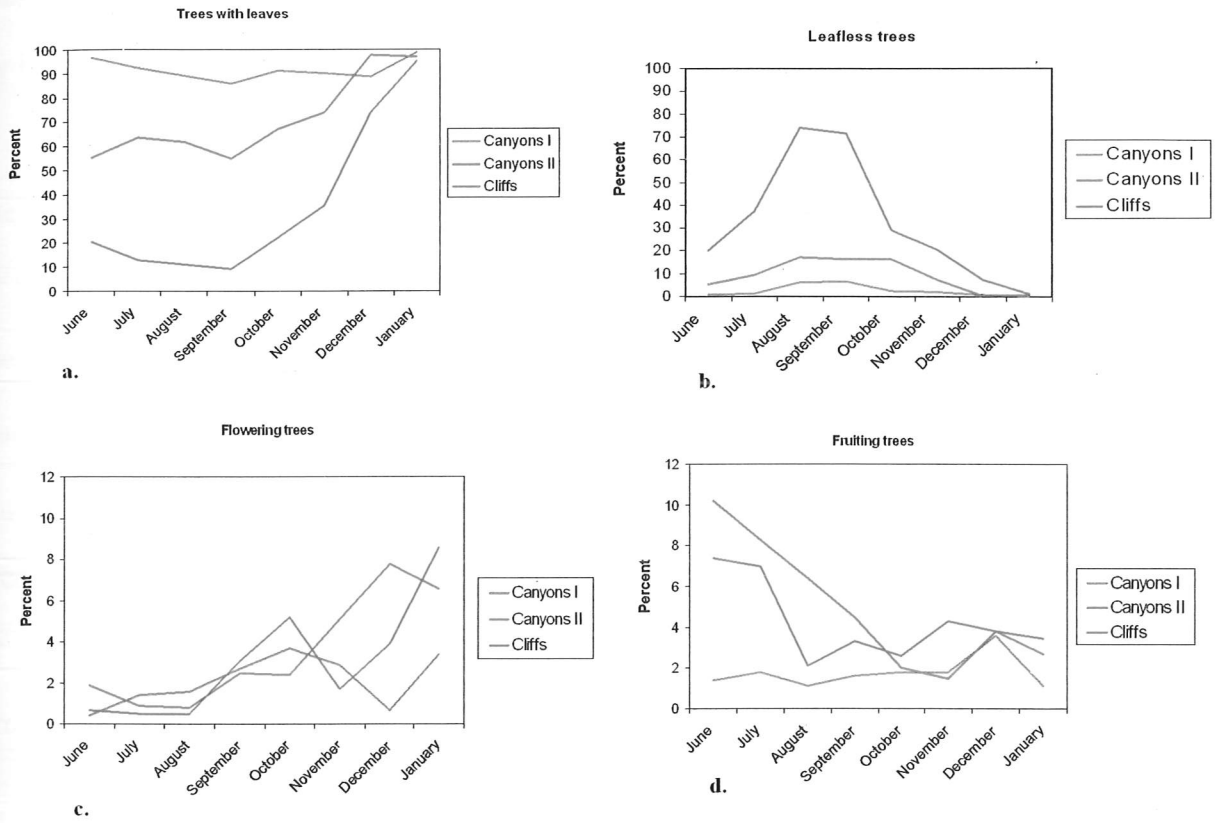

Figure 16. Phenological pattern of the sampled trees in the different habitats. See text for further details.

Systematic phenological sampling did not occur on the Plateau. There were, just 3 complete months (July, October and November) and two incomplete ones (May and June), thus hampering comparisons. Nevertheless, it presented a similar pattern to the Cliffs, although during the dry season up to 84.7% of trees in the Plateau were leafless compared to a maximum of 71.8% of the trees along the Cliffs, indicating that water shortage was markedly higher in the Plateau.

In the deciduous habitats (Cliffs and Plateau), some trees species kept the leaves throughout the dry season. For instance, in the Plateau *Hymenaea aurea*, *Maytenus* sp. and cf. *Eugenia* sp., did not shed their leaves. While along the Cliffs, species such as *Talisia esculenta*, *Capparis flexuosa* and cf. *Eugenia* sp. kept the leaves during the dry season. In the case of *T. esculenta* and *C. flexuosa* they flushed

with new leaves during the dry season, a possible mechanism to avoid leaf predation by herbivorous during the rain season.

The habitat along the Cliffs has peculiar 'islands' where most of the trees kept the leaves in the dry season (Fig. 17). These places probably had a higher availability of water, and many of the trees species found there were species commonest inside the Canyons (e.g., *Pouteria* spp., *Eugenia* sp., *T. esculenta*, *Guettarda* sp. etc). In a trail along the Cliffs with about 5 km extension, which I used for tracking the capuchin monkey group, I found seven of these small green islands. These islands were not large and their area ranged from less than 0.01 ha (8 x 10 m) to about 0.1 ha (8 x 110 m). The distance between the islands varied from 100m to 800m and they probably constitute an important resting and/or feeding place during the dry season.

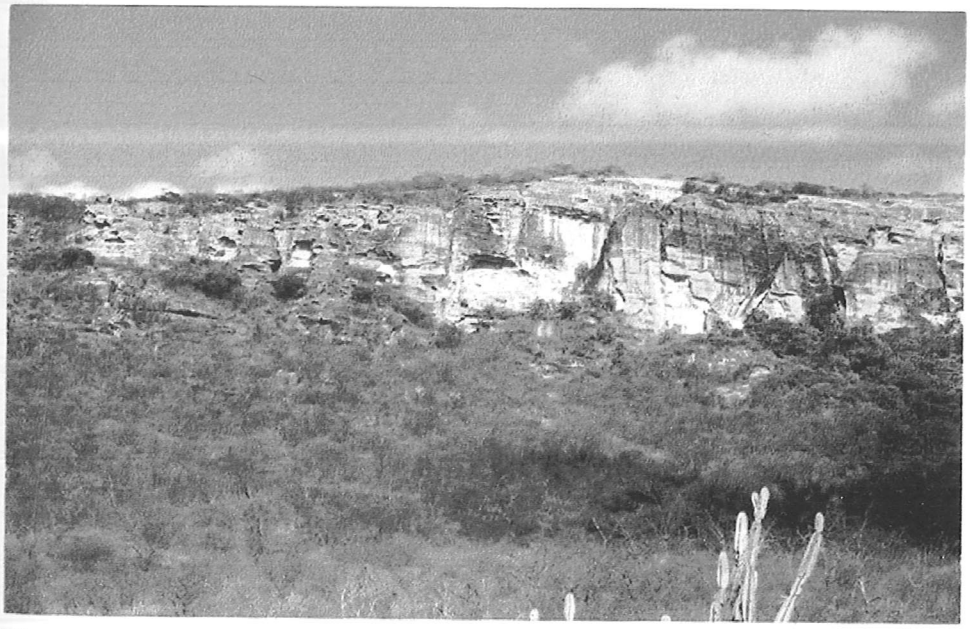

Figure 17. View of the Cliffs during the dry season. Note the deciduousness of the vegetation and one of the green 'island' on the right side. The cactus on the right side is a *Cereus jamacaru*.

Phenology and fruit availability for vertebrates

Tree species producing fruit with an abiotic dispersal type had a higher number of individual fruiting in the dry season (Fig. 18a.). This is an expected result, since during the dry season most trees were leafless and this was an optimal condition for the dispersal of fruits, when they can be dispersed for longer distance (e.g. van Schaik *et al.*, 1993). Although the high production of abiotic fruit in the Canyons II was somewhat unexpected, it resulted from the great density of 'pioneer' trees such as *Mimosa* spp., *Acacia* spp. and *S. spectabilis* along areas recovering from past disturbance (see Janzen, 1988).

A more interesting result was the considerable number of trees producing zoochoric fruit during the dry season in the Canyon habitats and, particularly in the Canyons II, there were more trees bearing zoochoric fruit in the dry season than in the wet season (Fig. 18b). Overall, the Canyon habitats seemed to have a relatively constant availability of zoochoric fruit throughout the year. The Cliffs habitat, on the other hand, had a strikingly high number of trees producing fruits during the wet season, while having the lowest density of trees bearing zoochoric fruit through the dry season (Fig. 18b). An important detail, however, was the overall low proportion of the trees with zoochoric dispersal type producing fruit in these habitats along the months. For instance, in the Canyons II the proportion of trees bearing zoochoric fruit varied monthly only between 4% and 6% of the total trees with zoochoric dispersal type (n= 708) and along the Cliffs it ranged from 4% in the dry season to 16% during the wet season (n= 200). This low crop availability to animal dispersers probably was a consequence of the irregularity and low rainfall in 2001 by comparison to 2000 (Chapter II).

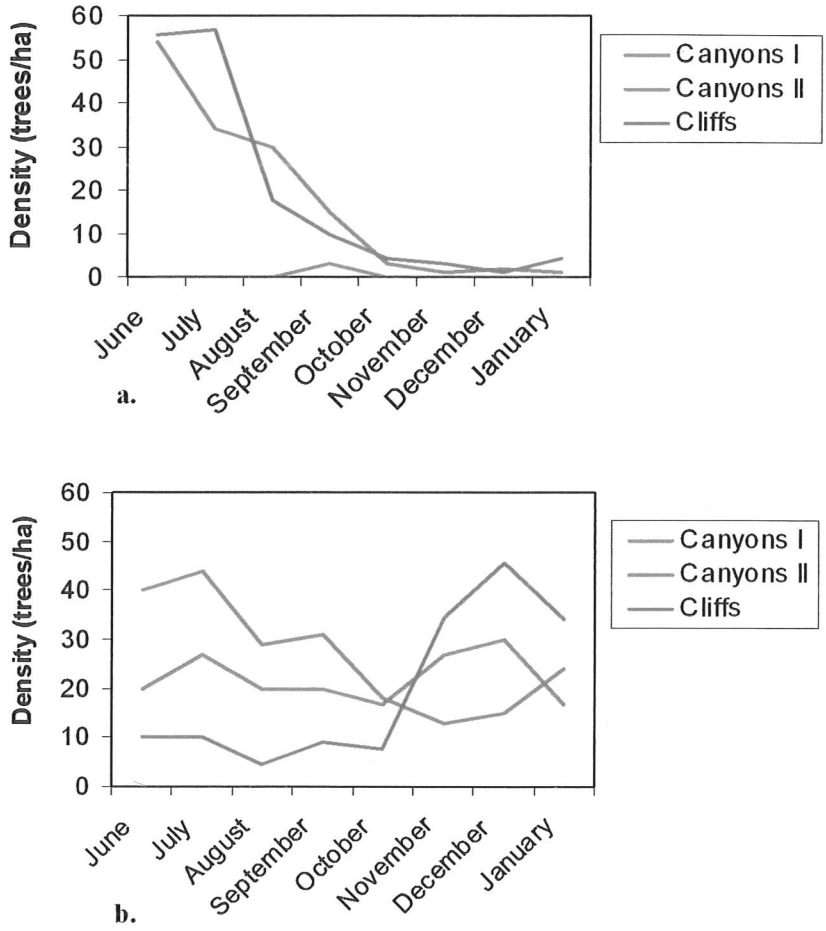

Figure 18. Density of trees with abiotic (a.) and zoochoric (b.) dispersal types producing fruit during the phenological sampling period.

The most important fruiting trees for the vertebrate community, based on their density in the area and potentially high number of species eating their fruit, were *Eugenia* sp., *Erythroxylum* spp., *Trichilia* sp., *Prockia crucis* and *Zizyphus joazeiro*. All of these species fruited in the wet season, but in 2001-2002 most of them failed to fruit, the only exeption being *P. crucis* and *Z. joazeiro*. One of the first species to have ripe fruits, from December to January, was *Eugenia* sp. By the end of January 2001, the Canyons I were carpeted with its fallen fruit. *Prockia crucis* had ripe fruit for

about two months (December and January), while *Erythroxylum* spp. and *Trichilia* sp. had an overlapped fruit period, bearing ripe fruit from middle of January to beginning of February. In April *Z. joazeiro* was practically the only plant along the Cliffs with edible fruit for a large number of vertebrates. This species seemed to be an important food resource for mammals (mainly primates) and larger birds (such as *Penelope* spp.), which feast on the copious fruit production of this tree and probably put on weight to face the dry season. This tree was commoner in sandy soils and usually was bearing ripe fruit from March to end of April.

During the dry season, the production of fleshy fruit was limited to a small number of trees in the different habitat and many species were uncommon or had a distribution limited to the Canyons habitat, such as *Styrax* sp., *Cybianthus* sp. and an unidentified Myrtaceae tree. In the Cliffs habitat, important fruit resources during the dry season were *Brosimum* cf. *alicastrum* (ripe fruit in July), and *Copaifera* cf. *langsdorfii* (ripe fruits in May-June). Another important food resource for the vertebrate community during the dry season was the fruit of the terrestrial bromeliad *Bromelia plumierii*, which had ripe fruit by the end of May. This species occurred at distance from 100 m to 1.3 km from the Cliffs, in sandy soils. Even though it was not found in the vegetation plots, it seemed to be very frequent along the Cliffs within the mentioned distances and in areas with an apparent higher water table level. Perhaps the most important tree species for the frugivorous vertebrate was *Ficus gomelleira*. This fig tree was relatively common along the Cliffs and especially inside the Canyons and, due to its asynchronous fruit production, these trees had available fruit in both the dry and wet season (see Chapter V). The forest on the Plateau apparently had only a single species producing fruit during the dry season, *Swartzia flamengii*, which had ripe fruit by end of September. Overall, the dry season was a critical

period, with few species and a low density of trees producing fleshy fruits in the different habitats.

DISCUSSION

The vegetation structure and species composition clearly define the three main habitats sampled. These different habitats, except most of the Plateau, present a great heterogeneity in the terrain, both from geological origins and human past activities, and this variability was reflected in the pattern of tree diversity and to some extent the forest structure in the different areas.

Interestingly, the pattern of β-diversity or species turnover is high inside the Canyon habitats, but this is probably due to past human disturbance. This high β-diversity provides an 'optimum' for increasing diversity of animal species and since the Canyons contain a higher number of zoochoric trees and a considerable number of these trees produce fruits during the dry season, these traits probably make the Canyons a keystone habitat (see Tews *et al.*, 2004) for the faunal community of the area. It is possible, that the distribution and location of this habitat in the area could affect the ranging pattern of primates and other mammal and bird species as well.

Comparison with other dry forests: how different is the Caatinga dry forest?

Tropical dry forests have a much lower diversity than wet forests (Murpho and Lugo, 1986) and the Caatinga is no exception, but Caatinga dry forest seems to present a lower diversity than other Neotropical dry forests. Lemos and Rodal (2001) report values of Shannon index (H') for 22 sites spread throughout the Caatinga

ranging from 1.64 to 3.36 and average of 2.47 (from values of Table 2). These values are lower than those observed in the dry forest of Santa Rosa National Park, Costa Rica, by Sorensen *et al.* (2000). In this area these author found a value of H' ranging from 2.15 to 5.22 (average of 4.4, n=13 sites). Differences in sampling methods could explain some of these differences. Nevertheless, data originated from similar 0.1 ha sampling protocol suggest that the Caatinga dry forest has lower tree diversity in relation to other Neotropical dry forests.

For instance, Trejo and Dirzo (2002) reported in 20 sites of Mexican dry forests an average value of 58 species/0.1-ha plots. These values are far above from what I found in my study area. Neotropical dry forests in general have an average number of 49.9 species per 0.1 ha plots (data from Appendix 2). In my study area I found an average of 18.3 species/0.1-ha plots. The number of species is significantly lower ($t= -8.7$; $df= 55$; $p<<0.001$) when compared with the number species/0.1-ha plots from other Neotropical dry forest (see Appendix 2). This could be an artefact of the differential number of trees observed across these 0.1-ha plots, since the number of species is related to sample size (Chapter II). However, even after calculating the Fisher's alpha values, which are independent of sample size (Chapter II), for all of these different sites and comparing with the values obtained in my study site, the difference between other Neotropical forests and Caatinga is still significant ($t= -6.4$; $df= 55$; $p<<0.001$). Historical events (forest conversion, hunting, fires, see Chapter II) could be affecting the forest structure and biodiversity in the area. However, other Neotropical dry forest also went through human disturbance (e.g. Janzen, 1988; Murphy and Lugo, 1986) and yet present a high diversity level. The low diversity of trees in the Caatinga dry forest in relation to other Neotropical dry forest can be an intrinsic property of the Caatinga as a whole, and is probably related to the highly

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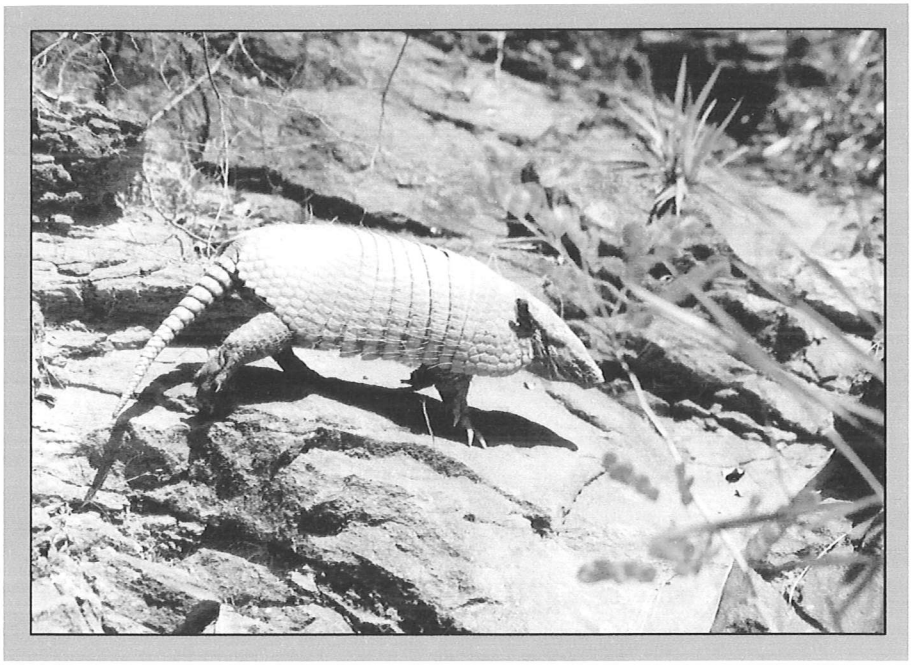
irregular rainfall regime (Chapter, II; Mares *et al.,* 1985; Reis, 1976). Thus, it is reasonable to assume that the Caatinga dry forest is harsher, in terms of food availability in space and time, than other tropical dry forests.

Apparently tree diversity is directly linked with the amount of rainfall (Gentry, 1988), although a series of other environment variables (e.g. soil fertility, amount of insolation and water soil availability) can explain higher or low levels of tree diversity for specific areas (Balvanera *et al.,* 2002; Trejo and Dirzo, 2002). What is important in the context of feeding ecology is that the irregular rainfall in the Caatinga leads many plant species to fail to produce fruits and this factor, coupled with a low tree diversity, is probably one of the main reasons for the impoverished mammal fauna observed in the Caatinga dry forest. Interestingly, 69% of trees in dry forest have zoochoric dispersion (Gentry, 1982: data from Table 8); even considering areas such as dry forest in Santa Rosa National Park, Costa Rica, the proportion of zoochoric tree species is high (64%) (Gentry, 1982; Janzen, 1988), while in my study area just 52% of trees had the fruits eaten by vertebrates. Possibly, this discrepancy results from the peculiar and erratic rainfall regime of the Caatinga. In the next chapter, I will explore how these local diversity and abundance of resources could affect the abundance and distribution of mammals.

SUMMARY

- The three main habitats of the park, Cliffs, Plateau and Canyons, present marked differences in water availability, geomorphology and levels of human disturbance, which affect the forest structure, species richness and floristic composition.

- The forest on the Plateau is more homogeneous in relation to species turnover (lower β-diversity than Canyons and Cliffs) and it has a significantly lower and simpler structure compared with the other habitats. The Plateau also has a significantly higher diversity of trees than do the other sampled habitats, probably due to its more pristine conditions.
- In relation to the habitat's importance for the vertebrate community, the Canyons contain a higher number of zoochoric trees and a considerable number of these trees produce fruits during the dry season. These traits probably make the Canyons a keystone habitat for the faunal community of the area. Another important aspect is that even during the extensive dry season Canyons can be a refuge for the vertebrate community, since most of trees keep their foliage there.
- Trees started to loose leaves in May and by August most of trees were leafless, but there were marked contrasts between the sampled habitats. During the dry season, a maximum of 20% of trees were leafless in the Canyons, while a maximum of 79% of trees along the Cliffs were leafless. Systematic phenological sampling did not occur on the Plateau. Nevertheless, it appeared to follow a similar pattern to the Cliffs. Fruit production was low during the study period and it can be linked to the markedly irregular rainfall.
- Overall, the diversity of Caatinga forest is significantly lower when compared to other Neotropical dry forests, even after controlling for possible sample size bias. The low diversity of trees in the Caatinga dry forest is probably a consequence of the highly irregular rainfall regime. I suggest that the Caatinga dry forest of Northeastern Brazil is harsher, in terms of food availability in space and time, than other tropical dry forests.



*Yellow armadillo (*Euphractos sexcinctus*) during midday walking.*

Chapter IV

MAMMAL ABUNDANCE AND ITS ENVIRONMENTAL DETERMINANTS

INTRODUCTION

The mammal community assemblage of Caatinga is composed of 80 species, most of them bats and rodents (Table 5). There are only two species of mammal endemic to the Caatinga (Chapter II) and some studies have described its mammalian fauna as being one of the poorest faunas of the tropics (Mares *et al.*, 1985; de Vivo, 1992). Interestingly the density of small terrestrial mammals (rodents) in the Caatinga is one of the lowest among the tropical arid and semi-arid environments (Mares *et al.*, 1985). General food scarcity may account for the low mammal density in Caatinga. Moreover, fruit trees are scattered, zoochoric fruits are produced only during the rainy season, and even so, some species can fail to fruit entirely if the rainfall is low in an annual cycle (Machado *et al.,* 1997; Chapter III).

The most common non-volant mammals are the crab eating fox (*Cerdocyon thous*), the rodents punare (*Thrichomys apereoides*) and prea (*Galea spixiii*), the yellow armadillo (*Euphractos sexcinctus*) and the marmoset (*Callithrix jacchus*) (Moura, 1999; Mares *et al.*, 1981). However, past studies on mammal densities and abundance in Caatinga are limited to small rodents and marsupials. Studies are still lacking on the density and abundance of medium-sized and large mammals and this is particularly surprising in the case of primates, which are diurnal and easily identifiable.

Table 5. Number of species of mammals from Caatinga forest*.

Mammals orders	Number of species
Marsupialia (opossums)	4
Xenarthra (anteater and armadillos)	4
Artiodactyla (deer and peccary)	3
Chiroptera (bats)	46
Rodentia (rodents)	14
Carnivora (carnivores)	7
Primates (monkeys)	3
Lagomorpha (tapiti or brazilian rabbit)	1

* Based on Willig and Mares (1989), Emmons and Feer (1997) and Chame and Olmos (1997).

The highest densities of mammals can usually be found in the granitic outcrops, hills and other rocky formations. These places provide a more "moist" environment than that of surrounding forests. The more mesic conditions are due to the presence of deep crevices and holes that can accumulate water (Streilein, 1982). Even during extensive drought, when most of trees lose their foliage, trees in these "refuges" keep their foliage; thus, they can play an important role in the survival of the small mammal community (Mares *et al.*, 1985). Wolff (2001) studied the seasonal distribution of some vertebrate (i.e. the lizard *Tupinambis teguixin*, the birds: *Penelope superciliaris* and *Cariama cristata*, and the mammals: *Puma concolor*, *Cerdocyon thous, Mazama gouazoubira, Tayassu tajacu* and *Dasyprocta prymnolopha*) in the Serra da Capivara National Park, and found that the majority of these species were found more frequently in the vicinity of water sources. Although he suggested that the availability of water sources can affect the distribution of most species and that, during the dry season, those species would migrate to areas with higher availability of water, such as the canyons; he did not evaluate the abundance of mammals in different areas of the park and its possible association with environmental factors.

The park has three main distinct habitats (Chapter II): Canyons, Plateau and the Cliffs facing the plains and each of these had a particular forest type (Chapter III). How do the environmental features of these habitats affect the mammal abundance? For example, the Canyons are wetter than the areas in the Cliffs and Plateau and, accordingly, their forest is taller and has a higher density of trees producing fruits eaten by mammals (Chapter III). Thus, one can expect a higher abundance of mammals in this type of habitat, not only due to the abundance of fruit resources but also to the availability of water.

The distribution of animals in the tropical forests has long been linked with environmental factors (e.g. Janzen and Schoener, 1968). Many of these factors can explain differences in the abundance of mammals in different areas (see Janson and Chapman, 1999, for review on primates). The most commonly-cited factor is food availability, which can be linked to soil fertility. Janzen (1974, cited in Emmons 1984) hypothesised that soil type was an important variable explaining abundance of animals, usually more fertile soils support a higher biomass of animal than nutrient-poor ones. Emmons (1984) consider the soil types differences as one of the most important environmental factor explaining the differences in mammalian abundance across different areas in the Amazon basin. She also suggests that competitive interactions over food resources can influence mammal abundance in different areas. Peres (1997a,b) has explicitly shown that primate abundance is significantly higher in areas with more fertile soils, i.e. white-rivers *Várzeas* forests, even considering the higher hunting pressure in these areas.

Forest structure also could account for variable mammal abundance; forest with a higher structural complexity, mainly a dense undergrowth, have higher mammal abundance (Emmons, 1984). Natural disasters are another factor influencing

abundance of mammals and other animals. For example, a severe drought in a dry forest of Madagascar had a negative impact on the population of *Lemur catta*, leading to a 31% decrease after two years following the drought (Gould *et al.*, 1999). The decline of vital food resources over time is another type of natural disaster that can lead to a considerable reduction in population size or even extinction such as that reported for *Cercopithecus aethiops* groups (Lee and Hauser, 1998).

One factor of paramount importance explaining variation in density among different species of mammals is the body size and the trophic level occupied by the species. Usually, population density declines with increase in body mass and trophic level (Damuth, 1981; Fa and Purvis, 1997; Robinson and Redford, 1986).

In this chapter, I will analyse the abundance of primates in greater detail for three key reasons; they are diurnal and relatively easy to spot, they are relatively larger mammals and there is a wealth of data dealing with Neotropical primate abundance and hence allowing for meaningful comparisons.

For fruit-eating primates, one of the most important variables affecting their density is the availability of fruits (Janson and Chapman, 1999). Robinson and Redford (1986) suggested that the density of *Cebus* would be linked to the fruit production in the forest. Indeed, Stevenson (2001) found that primate biomass in the Neotropics increases significantly with fruit production. Sorensen and Fedigan (2000) found that in the Costa Rica dry forests (Santa Rosa National Park) the density of *Cebus capucinus* increases in areas with higher fruit abundance. Consequently, in the Caatinga higher primate abundance can be predicted in the habitats with higher fruit productivity.

The small marmoset, *Callithrix jacchus*, is the primate species with the highest density in the Neotropics, according to the data compiled by Robinson and Redford

(1986). The high density of marmosets probably is a consequence of their morphological adaptations allowing an extensive use of exudate, chiefly during lean food times (Stevenson and Rylands, 1988). This adaptation is associated with a smaller home range area than that found for similar-sized callitrichids and thus to a more 'packed' distribution in different habitats. Moreover, they can attain high abundance in secondary growth vegetation and in disturbed habitats (Rylands, 1996). Thus, they are expected to be the commonest primate in the area and as the habitat along the Cliffs has a high density of exudate sources for the marmoset (*Anadenanthera colubrina*, *Croton sonderianus* and *Copaifera* cf *officinalis*), I suggest they will be much more abundant there.

Aims:

To evaluate the abundance of mammals in different areas of the park;

To estimate the primate population in the area, and determine how they are distributed among the different habitats of the park;

And, finally, to assess how environmental factors could affect the distribution of primates.

METHODS

Estimating mammal abundance

I followed the general established procedures of line-transect methods (Brockelman and Ali, 1987; Buckland *et al.*, 2001) for the survey of mammals. For the census, I used 6 transects of different lengths established in the three main habitats of the Park (Table 6). Altogether, the trails had a total extension of 12.5 km and a total of 318.1 km of census was amassed over 12 months. During about three months (April to June 2001) two field assistants helped with the mammal census. Although the use of different observers conducting the line transect censuses can give biased results (e.g. Mitani *et al.*, 2000), it is a normal practice to use different people after training (Peres, 1999). Personally, I completed over 84.8% of the total km surveyed.

Table 6. Details of the trails censused. Note that the Plateau and Canyons had a higher survey effort.

Place	Habitat type	Transect length (Km)	No of months censused	Total Km walked
Baixa Grande	Cliffs	1	12	22.3
Jurubeba 1	Cliffs	0.45	4	4.5
Jurubeba 2	Cliffs	0.7	9	13
Baixao da Vaca	Canyon	1.4	10	33.6
Esperacanca	Canyon	1.65	12	66
Zabele	Plateau	7.3	11	179.2

A reliable estimate of density is based on the number of sightings (minimum N= 40), which depends on transect length and sampling effort. Generally the transects in most surveys of mammals, particularly primates, have a standard length of around 3-4 km (Peres, 1999), but due to the characteristic topography of my study area, with a rugged terrain and canyons of different sizes and shapes, it was unfeasible to have

long transects except in the more level sandstone Plateau. This could be circumvented by establishing a number of short transects in the same habitat type; the density would be calculated from the sum of the different transect lengths censused. Due to logistical problems (namely lack of field assistants and limited time available to census each existing transect each month), however, this design turned just into wishful thinking.

Establishment of the transects

I started the transects at random places, except for those inside the canyons. I tried to optimise the sampling effort and time spent in the field by choosing the canyons with the largest length, Esperanca at ~ 2km and Baixao da Vaca at ~ 1.5km, and for their relative proximity to each other (about 6 km distant). In Esperanca Canyon there was an old cattle trail inside, and I used part of this trail for the census. When the trail deviated from a straight line I cut the vegetation trying to maintain a relatively straight line. In the Baixao da Vaca Canyon there was a relatively straight trail entering the canyon; park guides and tourists occasionally used this trail and, as a consequence, some mammals species there were more tame, e.g., the rodent *Kerodon rupestris*, but there was no provisioning in the area. In both Canyons the trails followed their contour and at some points there are deviations of more than 40^0 from a straight compass bearing.

The Baixa Grande trail ran parallel to the Cliffs at distances ranging from 30m to 250m. Most of this trail followed a straight line, but when cutting it I needed to make detours around big rocks, due to the rugged terrain, and at one point the vegetation was quite impenetrable leading to further detour. The Jurubeba 1 trail was cut perpendicular to the Cliffs and at its end there was a parallel trail running just by

the Cliffs, opened by the park management. I also used this parallel trail for the census (Jurubeba 2 trail). Both Jurubeba trails were about 6 km distant from the Baixa Grande trail.

In the sandstone Plateau I used an old trail with a length of about 20 km, located almost in the middle of the Park, bisecting the Plateau from East to West. This trail was made more than 80 years ago and was used by hunters and old inhabitants of a small village (around 200 people) located inside the park. When I started the censuses the inhabitants had been removed from the park for more than 4 years. This trail had been used for a study on the carnivores in the park by another researcher about 6 months before I started the census. I established the beginning of the census transect 2 km from the trail start, where no signal of past human activity could be detected. The Plateau trail was relatively straight, with a width of about 1 m and at some points 1.5m. Many mammal species used the trail for moving; for example in the rainy season, it was common to see tracks of peccaries, armadillos, foxes, puma and deer.

The trails were marked at 50m intervals with yellow coloured plastic flags, to facilitate annotation of transect length when a animal was seen and also as a point to stop and wait for a while before moving forward. The trail was walked slowly at a pace of about $1km^{-h}$ and both sides surveyed. The transects were walked at least once a month both in the morning (from 06 h) and in the afternoon (from 14 h) in order to avoid bias in sampling animals that could be more active during the morning or afternoon. In trails with a length $\geq$ 1km I usually waited at the end of the trail until 14 h or later and then returned doing the afternoon census.

During the census, data on species identity, group size, and opportunistic data on activity and sex of the animals were noted, as was the location relative to the transect line, distance to observer and angle in relation to the trail.

Dung beetle as an indirect clue for mammal abundance

An alternative and indirect way to compare different areas in relation to mammal abundance is to assess the diversity and abundance of dung beetles. The main food resources for the larvae of the dung beetle are dung and carrion. Thus, the general abundance of mammals sets the level of resources for the dung beetle community in any particular area (Hanski and Camberfort, 1991). If one area has a higher density or biomass of mammals, the abundance and diversity of dung beetle will be higher in that area. This method has not yet been tested in the Neotropics and thus should be viewed with caution, but logically it could provide excellent clues as to mammalian abundance in the different types of habitats I studied.

For assessing dung beetle abundance, I devised a trap consisting of a plastic container with a diameter of 16.6 cm and 20 cm deep, having a smaller plastic container for the bait (meat or dung) in its middle. In order to protect the apparatus against armadillos or other vertebrates that could eat the insects inside, I covered the traps with a wood disc, perforated with 1cm-diameter holes so that the smell of the bait could spread. I set up these traps along the Cliffs (Jurubeba 2 and Baixa Grande trails), Canyons (Esperanca and Baixao da Vaca) and Plateau. For each trail I randomly chose a starting point and from there I put 12 traps in line spaced 20 metres from each other. I baited the traps bimonthly using human faeces or meat, so that 6 traps were baited with meat and the other 6 with dung. The order that each trap received one of the two different types of baits was chosen at random. After two

nights I returned to the baited traps and collected all animals caught inside. Occasionally, after taking notes, I released the giant ant *Dinoponera quadriceps* and lizards that I had either already identified or which I had collected previously.

Analyses

Mammal abundance

The commonest and most robust estimator used to assess the density of animals, and particularly mammal density from the line-transect surveys, is the distance sampling method as delineated by Buckland *et al.* (2001) using the computer program DISTANCE. This method requires a substantial sample size, however, ≥ 40 sightings or in some cases at least 20 sightings (Peres, 1999) to produce reliable estimations of density. Frequently, in tropical forests, the number of sightings is below the minimum for estimation of reliable densities and this seems to be common for primates (e.g. Chapman and Chapman, 1999). Moreover, to obtain at least 20 sighting of primates groups in a habitat such as the Caatinga, I would probably have to walk the transects for maybe several thousands of kilometres, which was completely unfeasible due to financial and time constraints and lack of field assistance. One option for estimating the density is to use a strip width derived from pooling the sightings of all mammals observed, but this approach has not been well studied and could lead to biased results.

In order to overcome those problems I decided to use the number of sightings per 10km walked. This 'encounter rate' is an useful way to estimate mammal abundance in diverse types of habitats and many published papers on mammals abundance, mainly on primates, have used encounter rates for comparisons between different habitats (e.g. Carrilo *et al.*, 2000; Chiarello, 1999; Emmons, 1984; Lopes

and Ferrari, 2000) or to control for differential sampling effort in different areas (e.g. Peres, 1997a).

As many studies on Neotropical primates provide both the density (individuals/km^2) and encounter rates (groups/10km walked), I regressed these published data for *Cebus apella* (Appendix 4) in order to estimate the density of *Cebus* in the Park. Unfortunately, comparable density data were unavailable for *Callithrix jacchus* and *Alouatta caraya*. For fitting the regression line, I used data only from studies that used the program DISTANCE for estimating density, since the statistics behind this program are robust and thus can provide fairly accurate estimation of density (see Buckland *et al.*, 2001).

Dung beetle abundance

The Canyons and Cliffs had double the sampling effort of the Plateau. Moreover, some areas (Plateau and Jurubeba 1) had just 5 months of sampling due to logistical problems. Different sites with differential sampling effort could lead to confounding comparisons, since the abundance of dung beetle increases with the sampling effort. Thus, in order to correct for possible biases I multiplied the values of the Plateau by two and for all of the areas I divided the total number of individuals by the number of months sampled in each area, giving a sampling rate.

I used the sampling rate for carrying out all comparisons. Differences in species richness amongst the habitats were evaluated with diversity indices (Chapter II), but, as the sample effort varied among the three main habitats, I used pairwise comparisons to reduce bias. The identifications of the different beetle species are very gross and since I lumped possibly more than 10 species just as 'unknown', the results

regarding species richness differences in dung beetle community should be viewed with caution.

RESULTS

The Canyons had the highest number of mammal species recorded (18), while in the Plateau and Cliffs I found evidence (direct and indirect) of at least 14 species (Table 3). During the mammal censuses, many of the species listed in table 3 were not observed. Some species, due to their secretive habits such as *Coendu prehensiles*, an arboreal and nocturnal rodent, and the carnivores in general were rarely observed. Other species such as *Myrmecophaga tridactyla* and *Tolypeutes tricinctus* are endangered species and already very rare in the area. Two species of armadillos (*Dasypus novemcinctus* and *Euphractus sexcinctus*) are apparently very common, chiefly in the Plateau area where I frequently saw theirs tracks. In the Plateau area *D. novemcinctus* is the main prey item for pumas, accounting for 70.4% of the prey species found in puma scats (Wollf, 2001), which reflect the higher abundance of this armadillo species in the Plateau, but armadillos were not recorded during the diurnal census. *D. novencinctus* has nocturnal habits, and I saw one once. Moreover, they have a good sense of smell and hearing, running away as soon they sense someone around. On the other hand, time of day could influence the probability of seeing *E. secinctus*. By contrast to most species of mammals, this armadillo was more active during midday (see Schaller, 1983 for similar result), when I was usually not doing the census. Thus, the peculiar habits of these armadillos species made them difficult to observe during the census. Another factor, that perhaps reduced the probability of detection of terrestrial mammals, is that part of the trails along the Cliffs and inside the canyons had loose rocks on the ground, making it impossible to walk silently and

this probably scared some species away (see Emmons, 1984 for similar problems). Nevertheless, the lack of sighting of many diurnal species listed in Table 7 is more parsimoniously explained by their exceptionally low density in the area.

Table 7. Distribution and species of mammals in the different habitats of the Park based on direct (sighting) and indirect evidences. D= dung; T= tracks; S= sighting; C= carcass. Weight and species name based on Nowak (1999). Primate weight based on Smith and Jungers (1997).

Species	Weight (kg)	Cliffs	Canyons	Plateau
Panthera onca	90-120			D
Puma concolor	60-103	D, T	T	D, T
Felis pardalis	11-15		T	T
F. tigrina	1.7-2.7	S	S	T
Herpailurus yagouaroundi	4.5-9		T	S
Cerdocyon thous	6-7	S	D, S, T	S, T
Procyon cancrivoros	2-12		T	
Eira barbara	4-5		S	
Conepatus semitaeniatus	2.3-4.5	C, S	S	S, T
Dasyprocta cf.*prymnolopha*	1.3-4	S		S, T
Coendu prehensiles	1-5		C	
Kerodon rupestris	0.9-1	D,S	D, S	
Eupractes sexcinctus	3.2-6.5	S; T	T	S, T
Dasypus novencinctus	up to 10		T	S, T
D. sepemcinctus	?	S		
Tolypeutes tricinctus	1.4-1.5			S
Tamandua tetradactila	2-7	D; S; C	S	S, T
Mymercophoga tridactyla	18-39		T	
Tayassu peccary	14-30	S, T	T	S, T
Mazama guazoubira	8-25	S		S, T
Cebus apella	2.5-3.6	D, S	D, S, T	
Alouatta caraya	4.3-6.4	D, S	D, S	
Callithrix jacchus	0.36-0.38	S	S	S

Line-transect census

The relative mammal abundance (Encounter rate) exhibited a distinct pattern in the three habitats surveyed. The Canyons had a larger relative abundance of mammals than did the other habitats (Fig. 19), but 67.3% of the mammal abundance in the Canyons was due to the rodent *Kerodon rupestris*, while primates account for

81.9% of the relative mammal abundance along the Cliffs (Table 8). Despite the significantly higher sample effort in the Plateau, just four species were seen there, while eight species of mammals were observed along the Cliffs and inside the Canyons during the line-transect surveys.

Among the primates, *Cebus* was found at higher abundance along the Cliffs, while the howler monkeys and marmosets were seen more frequently inside the Canyons (Table 8). The higher frequency of marmosets in the Canyons, however, was apparently due to a repetitive count of a single group living in secondary vegetation in Esperanca Canyon.

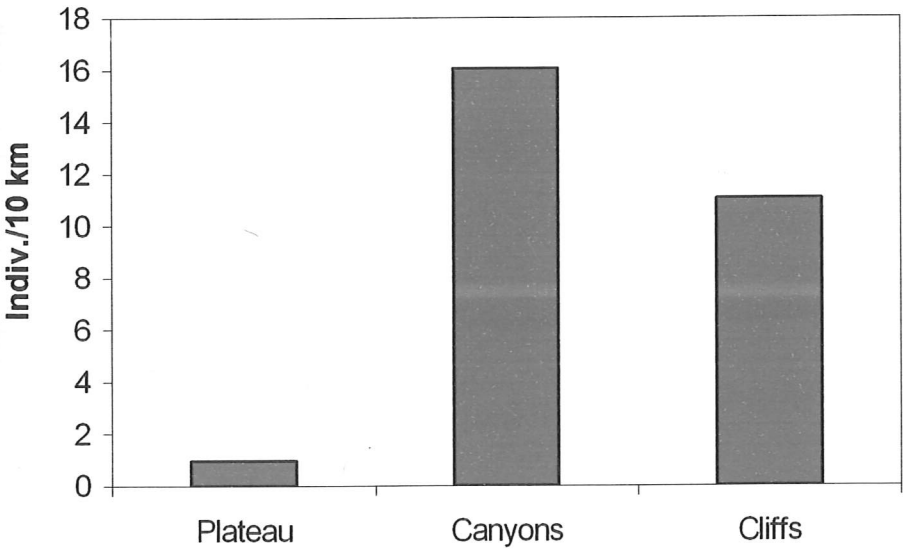


Figure 19. Relative abundance of mammals in the three main habitats of the Park.

Table 8. Encounter rate, individuals/10 km walked. Values inside ( ) represent number of sightings.

Species	Encounter rate		
	Cliffs	Canyons	Plateau
Cerdocyon thous	0.5 (2)	0.1 (1)	0.06 (1)
Eira barbara		0.1 (1)	
Conepatus semitaeniatus	0.25 (1)	0.1 (1)	
Dasyprocta cf.prymnolopha	0.25 (1)		0.39 (7)
Kerodon rupestris	0.25 (1)	10.94 (109)	
Tamandua tetradactyla		0.1 (1)	0.06 (1)
Tayassu tajacu	0.5 (2)		0.45 (8)
Mazama guazoubira	0.25 (1)		
*Alouatta caraya**		0.4 (4)	
*Callithrix jacchus**	1.0 (4)	0.7 (7)	
*Cebus apella**	1.5 (6)	0.2 (2)	

* For primates values represent groups/10 km.

Mammals and the dung beetle community

I collected a total of 1,831 dung beetle, of which 57.2% originated from the pitfalls set by the Cliff habitat. After correcting for sample effort, the Cliffs still remained the area with the greatest number of dung beetles captured (Fig. 20). The vast majority (97.5%) of dung beetles were caught during the wet season.

The abundance of dung beetles is linked to that of mammals. Although the highest relative abundance of mammals was in the Canyons, it was mainly due to *K. rupestris* and the dung beetles apparently did not use the dung pellets of this rodent. I frequently saw petrified dung of *K. rupestris* on the Cliffs and Canyons' rock walls. The greater number of dung beetles caught along the Cliffs probably reflects the higher abundance of primates in this type of habitat.

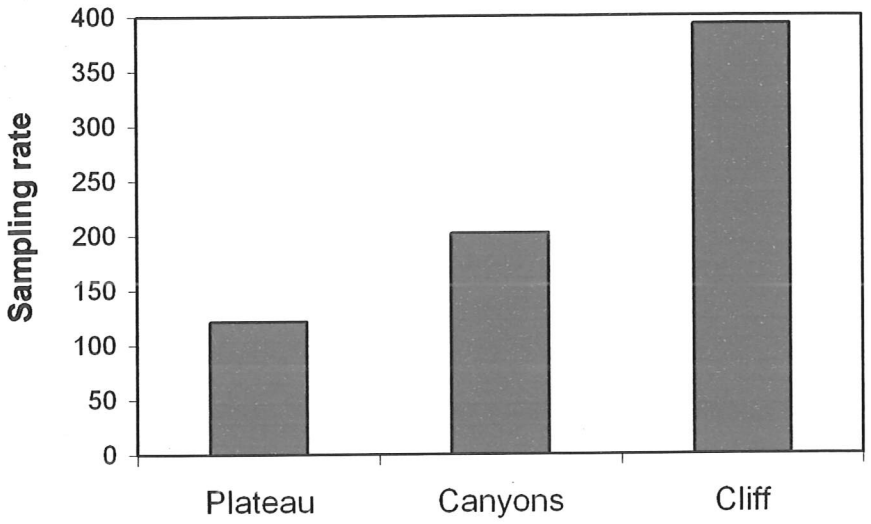


Figure 20. Total capture of dung beetle in the 3 different habitats. There were significant differences among the habitats (χ^2= 161.1; df= 2; p<< 0.001) and the Cliffs had a significant higher amount of dung beetles than did the other habitats (*post hoc*, p<0.001).

The habitat with the highest diversity of dung beetles was the Plateau (Table 9). It attained a significantly higher diversity than the other habitats (t test, p< 0.001), except when compared to the dung beetle community of the Jurubeba trail that was moderately similar to Plateau (t= 1.79; p= 0.07). The higher diversity of the Plateau habitat could be associated with the pristine conditions of this habitat, but these results should be viewed with caution, since most of the dung beetle identifications were gross and many species were lumped as unknown.

Table 9. Dung beetle species richness in the different habitat sampled.

Diversity index	Plateau	Canyons		Cliffs	
	Zabele	B. Vaca	Esperanca	B. Grande	Jurubeba
# of individuals	177	481	125	790	258
# of species	13	13	10	11	12
Shannon's H	1.992	1.434	1.287	0.998	1.891
Fisher's α	3.233	2.462	2.558	1.809	2.606

Primate group size and occurrence in the different habitats

During the line transect census I saw a total of 8 groups of *Cebus*, with an average size of 4.8 individuals (range 1 to 9). This value cannot be taken as accurate, since the inter-individual distance among group members was usually high (see Chapter V) and many times foliage or big outcrops concealed part of the group. Considering all time I spent in the area, from October 2000 to March 2002, the most frequent group of monkey I saw was *Cebus*. I recorded 40 observations of *Cebus*, with an average group size (±SD) of 8.8 ± 4.3 individuals (maximum group size=16; mode = 13). On many occasions, however, I was unable to determine if it was the same group or a different one was being sighted, because the home ranges of capuchin monkeys in the area had quite extensive overlap. For instance, in the Oitenta area, where I followed a group of *Cebus* (Chapter V), at least three different groups passed through the area. A group from Baixa Grande area sometimes travelled more than 5 km, passing by Oitenta area moving in the direction towards 'Caldeirao do Gato' canyon, that was frequented by another *Cebus* group. Nevertheless, the average group size of about 8 individuals/group is realistic and within the normal range reported for *Cebus apella* (Appendix 3). During the censuses, *Cebus* was much more frequently observed along the Cliffs than in the other habitats (Table 8).

Callithrix jacchus had a smaller group size than *Cebus*, with an average (±SD) of 2.9± 1.67 individuals/group (n=30 including observation from censuses, maximum group size= 7, mode= 2). During the line-transect census I saw a total of 11 marmoset groups, but on six occasions the group I observed seemed to be the same as it was of similar composition and in the same area. The common marmoset was the most widespread primate in the area, occurring in more degraded areas, in shrub vegetation and even in the Plateau, where I saw a small group of about 4 individuals. The place

where I observed them was a kind of 'depression' area that probably could accumulate more water than the higher Plateau. Accordingly the vegetation was taller and had species such as *Acacia* cf *paniculata* and *Croton sonderianus* from which the marmosets can exploit exudate. The area the marmoset seemed to be using was about 2 km away from the transect trail and, when censusing the trail in the Plateau, I never saw or heard any calls of marmosets.

Howler monkeys, *Alouatta caraya*, were rarely seen and I heard their characteristic calls only twice. I saw them on ten occasions (including observations from the line-transect census) and their group size was the smallest of the primates occurring in the area with an average (±SD) of 2.8 ±2.7 individuals (n= 10; maximum group size= 10; mode= 1). When doing the line transect census, I observed *Alouatta* only in Esperanca canyon, which had a taller and better preserved forest in relation to Baixao da Vaca canyon (see Chapter III). On two occasions I saw *Alouatta* along the Cliffs; in one case in Baixa Grande area, a group with ten individuals on a *Zizyphus joazeiro* tree eating its fruit and the other case was a single male eating the leaves of *Tabebuia impetiginosa* in the Oitenta area. On the transect censuses I saw howler monkeys on four occasions, all of them inside Esperanca Canyon, and they had an extremely low abundance (Table 8).

Cebus density and comparisons with other forests

The number of groups observed was very low for estimating density through specific computer programs (e.g. Distance). Using data from other studies on the relationship between encounter rate and density, however, allowed me to calculate the regression line (Fig. 21 and Appendix 4) and its algorithm for *C. apella* and hence estimate the density for the surveyed area. Through this approach, I estimate an

average of 7.5 individual/km^2, but if I take into account only the area where the monkeys are found (Cliffs and Canyons) the density rises to 11.2 individual/km^2. Despite the weakness of this approach, these values are consistent with other evidence. For instance the group I studied in detail had a home range of about 135 ha (Chapter V), or a density of 7.1 individuals/km^2. Nevertheless, these data must be viewed with caution, since the group I followed was provisioned and probably had a smaller home range than non-provisioned groups (Chapter V).

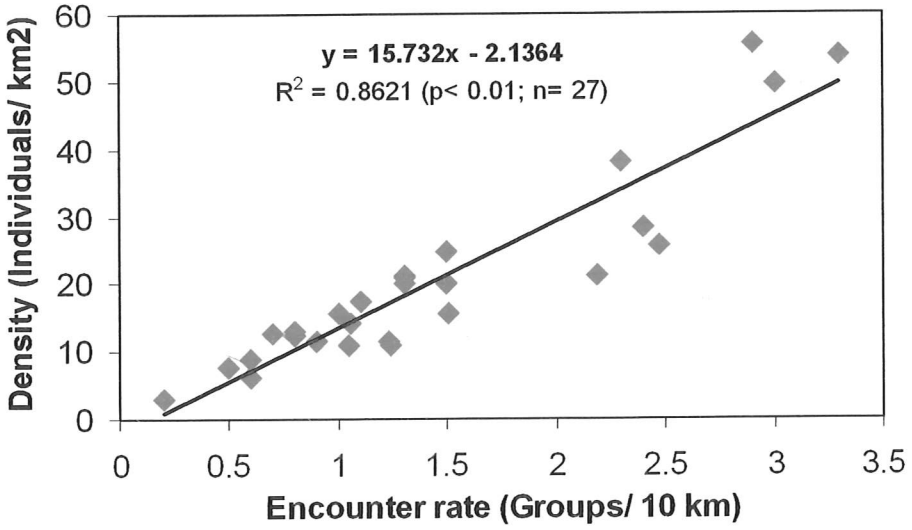


Figure 21. Relationship between encounter rate and density for *C. apella* in surveyed sites located in the Amazonian and Atlantic forests.

C. apella occur in the Amazonian forest at an average (±SE) 22.5 ±3.4 individuals/km^2 and in the Atlantic forest at an average of (±SE) 14.7 ±2.57 individuals/km^2. These values are considerably higher than the density I estimated in the Caatinga area of 7.1-11.2 individuals/km^2.

DISCUSSION

The lowest encounter rate of mammals was in the Plateau area. This habitat has a practically-pristine forest with higher plant species richness than other habitats (Chapter III), which could be associated with higher food availability, yet mammals were rare there. Several factors might affect the mammal encounter rate in the Plateau. Among the different areas surveyed, the Plateau was the most inhospitable. For instance in the rainy season, during two months (January and February) the density of horseflies (Tabanidae) was enormous, particularly in January when it was impossible to conduct censuses. During the height of the dry season, the forest in this habitat became almost leafless (Chapter III), and shade and protection from heat was minimal. The availability of water was negligible and restricted to a few temporary trunk holes. During the dry season, water was effectively unavailable in the Plateau and water availability is an important variable explaining the distribution of terrestrial vertebrates in the Park (Wolff, 2001).

Overall, the average encounter rate for the terrestrials mammals in the studied area of the Caatinga dry forest is somewhat similar to that reported for tropical rainforest, i.e. the Atlantic forest and the Amazonian forest, and similar to that for the dry Cerrado vegetation (Table 10). The relative abundance of large mammals, however, such as the brown brocket deer (*Mazama guazoubira*), agouti (*Dasyprocta* sp.) and collared peccary (*Tayassu tajacu*) is strikingly low in the Caatinga. Although this could be due to a lower availability of food resources in the area, it probably stems from a higher hunting pressure until the recent past. Primates are not hunted in the Caatinga and had a relatively high abundance, while the ungulates have the lowest abundance. In the Amazonian forest, where primates are hunted, the mammalian community in hunted forests tends to be dominated by small mammals (Peres, 2000).

Table 10. Comparison of the average encounter rate of selected terrestrial mammals in the Caatinga dry forest with those from rainforests. Data for Atlantic forest from Chiarello (1999), for the Amazonian forest from Thoisy (2000) and for Cerrado (Brazilian Savannah) from Schaller (1983, based on table 4).

Species	Caatinga forest (average)	Atlantic forest (average)	Cerrado forest (average)	Amazonian forest
Cerdocyon thous	0.22	0.08	0.18	--
Dasyprocta spp.	0.21	1.96	0.24	3.4
Eira barbara	0.03	0.06	0.03	0.2
Mazama spp.	0.08	0.73	0.22	0.1
Tamandua tetradactila	0.05	0.08	0.12	--
Tayassu tajacu	0.18	0.17	0.22	0.7

*Groups/10 km walked.

Comparisons of the relative abundance of terrestrial mammal species from Caatinga with similar species in other habitats are fraught with problems, however. Firstly, there is a great variability in faunal richness and food availability between the different forest types, which probably affects the abundance of different species. Secondly, the secretive habits of some species such as *Mazama* spp., *T. tetradactila* and *E. barbara* can make them hard to spot in forests with a dense foliage (see Schaller, 1983) or with a high canopy height, as is true of rainforests in general. Thirdly, most of species listed above are also active at night and, probably in the Caatinga, they are even more nocturnal since temperatures during the day are extreme, thus further hampering comparisons. And finally, this is the first study on the mammal abundance in the Caatinga dry forest and the dearth of information about terrestrial mammal abundance in Neotropical dry forests limits comparisons. Nevertheless, it is noteworthy that in the area where I carried out the study there is still a healthy population of carnivores (Wolff, 2001), many species of which have gone locally extinct elsewhere in areas of the Caatinga biome. *Kerodon rupestris*, an endemic mammal from the Caatinga, also has a healthy population in the park, being the most commonly-seen mammal in the area.

The primates were one of the commonest mammals in the area, and they are still present in much of the Caatinga region, although howlers and capuchin monkeys have gone extinct in some localities due to habitat alteration (Pers. observ.; Coimbra-Filho and Camera, 1996). One important aspect is that the primates in this dry forest are not hunted; they were relatively easy to spot and there are many published studies providing the relative abundance (encounter rate) for primates in other forests types, thus allowing adequate comparisons (see below).

Primate abundance and use of the different habitats

Cebus and *Callithrix* were the commonest primates in the area, while *Alouatta* presented the lowest abundance and they were effectively restricted to the Canyon habitat. *Cebus* predominate along the Cliffs, being by far the most abundant primate there, although in general they had a somewhat more restricted distribution throughout the park than did *Callithrix.* Primates were absent along the trail in the Plateau and the same explanations for the lower abundance of terrestrial mammals in this habitat (see above) could apply to the absence of primates. The lower height, mean of 4 m, of the forest in the Plateau (Chapter III) is another variable that could account for the absence of primates, facilitating predation by terrestrial predators such as the Felidae. Nevertheless, I observed capuchins venturing into the Plateau by the Cliffs a couple of times (Chapter V). The fact that I collected dung of howler monkeys with seeds of *Byrsonima* cf *gardneriana*, a species exclusive to the Plateau, suggests that they were also using the Plateau at least in the rainy season, perhaps as a short cut between canyons. Apparently all primates species were capable of using the Plateau area, but only around the borders of the Plateau/Cliffs.

The most puzzling result was that the highest abundance of primates was along the Cliffs, the habitat with the lowest density of trees producing zoochoric fruits (Chapter III). Ecological factors can play an important role in determining abundance of primates and food supply is supposed to be a critical component affecting the relative abundance of primates between areas (Chapman and Chapman, 1999; Brugiere *et al.*, 2002). Indeed, Stevenson (2001) found that, in the Neotropical primate communities, fruit productivity is the best predictor for primate biomass (and abundance). In the dry forest of Costa Rica, the density of *Cebus capucinus* is directly linked to fruit abundance (Sorensen and Fedigan, 2000). Thus, one would expect the highest relative abundance of *Cebus* and other monkeys inside the canyons, where the number of zoochoric fruiting trees is significantly higher than in the other habitats (Chapter III). Furthermore, the most probable place to find water holes or small water ponds during the dry season is inside the Canyons. Yet, primate abundance there was particularly low. One possible explanation for this discrepancy is to imagine the Canyons as islands with a distinct flora, but with a small area and a more limited abundance of food resources that could be depleted more quickly. Trees producing fruit eaten by the primates, however, have significantly higher densities inside the Canyons (see Chapters III and V) and fruit productivity seems to be much higher there. Moreover, during the harsh and extended dry season there were more species of zoochoric trees fruiting inside the Canyons than along the Cliffs. Perhaps the high abundance of primates, mainly *Cebus*, along the Cliff might be a consequence of moving between Canyons, but, if so, the encounter rate in the canyons should have been much higher, since this habitat had a higher sampling effort than did the Cliffs.

An important confounding factor, however, was that the Park management had put a small number of feeding station in some areas, provisioned with corn and

Manihot tubers, at distances ranging from 400m to 3 km to the Cliffs. These feeding station were established for improving the recovery of grey brocket deer, collared peccary and agouti populations, and obviously for capuchin monkeys it was an opportunity for access to food too good to miss. Howler monkeys and marmosets did not eat these provisioned foods. In the Baixa Grande area, the feeding station was about 1.3 km from the census trail and in Jurubeba area it was just 300m from the trail (Jurubeba 1). Clearly, the placement of these feeding stations might affect the distribution of *Cebus* in the area, but there is one feature of capuchin monkey biology and two crucial elements of the Cliffs habitat that minimises or removes the possible association of these feeding station with the higher encounter rate of *Cebus*.

First, the habitat along the Cliffs is very heterogeneous in terms of forest structure and geology, human disturbance, vegetation age and in some areas- with more shade and perhaps higher underground water availability- the vegetation is similar to that of Canyons. This kind of mosaic habitat increases the diversity and availability of food resources and consequently could support a large population of primates. In a primate community in the rain forest of Gabon, Brugiere *et al.* (2002) found that the populations of cercopithecines and colobines benefit from a more heterogeneous habitat, and are found at high density as a result.

The second point is related to a biological aspect of the vegetation along the Cliffs. About 70% of Cliff trees are leafless during the dry season. Perhaps trees that loose their leaves seasonally contain a lower concentration of chemical protection against herbivores (Coley and Barone, 1996); thus they would harbour a more diverse and abundant community of primary consumers. Usually, leaves with a short lifetime, i.e. less than six months, are relatively more palatable for herbivores and also have lower amount of chemical defences (Coley and Barone, 1996). Thus, the more

seasonal trees in the Cliff habitats could potentially harbour a higher abundance and diversity of invertebrates than the ones in the Canyon habitats, leading to a cascade effect in the abundance of secondary consumers. As invertebrates in general make up a great proportion of food intake in capuchin monkey diet (Janson and Boinski, 1992; Chapter V), then a habitat with a greater supply of this resource is likely to be used more extensively. This possible association between higher level of seasonality, greater availability of invertebrate prey and consequent increase in the abundance of capuchins is speculation at this stage. *Tabebuia impetiginosa,* however, the most commonest tree species along the Cliffs, by the beginning of the dry season had about 70-80% of its leaves eaten by insects suggesting low chemical defence. Additionally, when the leaves started to dry out before they fall, they become rolled up and spiders, cockroaches and other insects can be found inside. Thus, this area becomes an important foraging place for more insectivorous primates such marmosets and capuchin monkeys. Moreover, along the Cliffs there are some vital food resources for the monkeys which are not found in other habitats and some fruit trees that fruit only in the middle of the dry season. I will deal in more detail with these ecological aspects indicating higher availability of food along the Cliffs in Chapter V.

The average encounter rate for *C. apella* in the Caatinga forest was 0.57 groups/10km, while in the Atlantic forest and Amazonian forest they are found more frequently at an average of 1.47 and 1.42 groups/10km, respectively (data from appendix 4). These values are not significantly different (ANOVA, $F_{2, 32}= 1.27$; $p=0.29$). Unfortunately, surveys of *Callitrix jacchus* are lacking in wet forests. For *Aloutta caraya*, Schaller (1983) reported the occurrence of 21 groups living in different types of forest in the dry Cerrado vegetation of Central Brazil. From his data I calculated an average encounter rate of 1.22 groups/10km in the Cerrado. More

recently, Dvoskin *et al.* (2004) reported 7 groups living in gallery forest of the Argentinean Chaco; the encounter rate in this area was 1.46 groups/10km. These values were far above those that I registered in the Caatinga of 0.13 groups/10km. Overall the abundance of primates in the Caatinga dry forest is very low and almost certainly is a consequence of low abundance of food resources both in space and time (see Chapter III and V). Although human disturbance in the area is likely to have had its impact on primate abundance, the lack of similar studies in other areas of the Caatinga with different degrees of disturbance makes it imprudent to speculate about the extent of its effect on the primate community. A recent management strategy by the park direction, however, namely cutting lianas from trees in order to improve tree growth and prevent their death, has probably had a negative effect on howler population, albeit with good intentions. Lianas constitute an important resource for howlers in Amazonia forest (Santamaria and Rylands, in press) and Atlantic forest (Galetti *et al.*, 1994), and a reduction in the availability of different resources in an area already with a lower number of alternative food sources such as the Caatinga is likely will be deleterious.

Capuchins, marmosets and howlers: Generalists in the Caatinga dry forest and the ill fate of a quasi-herbivorous primate

Interestingly *Cebus* and *Callithrix* had the same average encounter rate (0.57 groups/10 km). Although marmosets were more widespread throughout the area, I was expecting them to be much more frequent as suggested in the introduction (they use disturbed areas, have a small body size and home-range). Robinson and Redford (1986) showed that larger primates tend to occur in low densities and abundance in comparison with smaller ones and their density is determined by the availability of

potential resources. The similar relative abundance of marmosets and capuchin monkeys in the Caatinga is perplexing because along the Cliffs an important source of exudate for the marmosets, the tree *Anadenanthera colubrina*, was the second commonest tree (Chapter III). Exudates are a rich source of carbohydrate and minerals for many species of Callitrichidae particularly for *Callithrix* and *Cebuella*, and are available year round (Lacher *et al.*, 1984). If invertebrate diversity and abundance is higher along the Cliffs (see above and Chapter V) and there is a higher abundance of food resources, i.e. exudate trees, why then were marmosets not found more frequently than *Cebus* during the censuses? Perhaps this could be a consequence of habitat partitioning due to feeding competition. Emmons (1984) emphasised that, in the more unfavourable habitats of the Amazon basin, smaller mammal species became rare, while the larger ones maintain their densities. She suggested that direct competitive interactions over food sources, mainly during of food scarcity, put small mammals at a disadvantage with respect to the larger species; for primates, she cites cases in Cosha Cashu, Peru, where *Cebus apella* troops displaced small primate species or prevented them from having access to fruit sources. Although this is a plausible explanation for the low abundance of marmosets along the Cliffs, it is unsatisfactory since marmosets had access to exudate, a resource not exploited by the other primates.

Another explanation could be linked to the generalist diet of *C. apella,* allowing them to use a greater number of resources in the Cliffs habitats than could the marmosets. This capuchin monkey species is generally widely distributed inhabiting a huge variety of forest types, and their success is associated mainly with a generalised and flexible diet (Fragaszy *et al.*, 1990). For instance Wallace *et al.* (1998) did not find any differences in group size and abundance of *C. apella* in two

different habitats sampled, while *Ateles* was much more sensitive to habitat type. They explain the almost ubiquitous presence of *Cebus* as due to their very generalised diet, but the same reasoning could apply to the marmosets, albeit with a more limited geographic distribution than *Cebus*. Marmosets do have a generalised diet and can be found in areas so modified and degraded that no other Neotropical primate can endure there. Perhaps this similarity in relative abundance between marmosets and capuchin monkeys along the Cliffs habitat was just a quirk of chance.

Nevertheless, overall low food abundance can have a negative impact on group size, e.g. by increasing mortality (Gould *et al.*, 1999). Thus, the comparison of group size of marmosets and capuchin monkeys living in forest with a higher availability of resources demonstrates how the harsh Caatinga environment affects these primates and provides more meaningful results.

The average group size for *C. apella* in the Caatinga was within the range reported for the Amazonian and Atlantic forests (Appendix 3). Indeed, there was no significant difference when I compared the group size in Caatinga to those from wet forest ($t= -0.87$; $df= 63$; $p= 0.38$)[1]. In the Cerrado vegetation, Schaller (1983) reported a group size of about 8 individuals ($n= 24$ groups).

Apparently the harsh condition of the Caatinga had a more deleterious effect on the group size of howler monkeys and marmosets. The average group size of *Alouatta caraya* in the Cerrado is 7.2 individuals ($n= 16$ groups, Schaller, 1983) and Thorington *et al.* (1984) reported a mean group size between 7.2 to 8.9 individuals in subtropical habitats of Northern Argentina. Dvoskin *et al.* (2004) reported an average group size of 5.7 individuals in the Argentinean Chaco. Zunino *et al.* (2001), in a

[1] When I excluded group size originated from line transects census carried out in the Amazonian forest and Atlantic forest, there was a slight trend for the group size in the Caatinga be smaller ($t= -1.74$; $df= 53$; $p= 0.087$).

more detailed analysis, found an average group size ranging from 3.5 to 12.4 individuals (n= 61 groups). These values are far above those I found in the Caatinga (2.8 ind./group). The mean group size for *A. caraya* in the Caatinga is significantly lower than those reported for Northern Argentina ($t= -4.61$; $df= 19$; $p << 0.001$)[2]. The marmoset group size also seems to be adversely affected in the Caatinga dry forest. It is significantly lower than the reported group size for *C. jacchus* living in different areas of Northeastern Atlantic forest ($t= -8.8$; $df=51$; $p<<0.001$)[3]

The low group size of howler monkeys in the Caatinga can be generally explained in terms of availability of resources. The leaves in the Caatinga forest, their main food resource, are available only for a short period of time (most of trees are leafless in the dry season) and fruit production is low and practically limited to the rainy season. It is also possible that inter-specific competition with *Cebus* is responsible for their unusually small group size in the area. For instance, Zunino *et al.* (2001) observed the smallest average group size for *A. caraya* in Northern Argentina in a forest that also had *C. apella* and suggested that interspecific competition could be an important variable explaining low abundance of howlers there. For the Caatinga, however, probably a series of factors, namely low availability of resources, habitat alteration and perhaps competition with *Cebus* contributed to the low density of *A. caraya*.

The small group size of marmosets in the Caatinga is more problematic to elucidate. There is the possibility that their population had suffered a decline in the more recent past as a result of a long period of drought (see Gould *et al.* 1999), which is relatively common in the Caatinga, leading to a prolonged crash in fruit production

[2] For the test I used the group sizes provided in table 2 from Thorington *et al.* (1984).

[3] I used the group sizes presented by Konig (1995) and Lazaro-Perea (1999).

that caused mortalities. Yet, this is not the most reasonable explanation, since they do have the ability to use exudate from trees and this skill has allowed them to survive in very unfavourable habitats (Stevenson and Rylands, 1988). Maybe their small size prevents them from moving to more favourable areas when resources become scarce, as do many primates during food bottlenecks (e.g. Peres, 1994a) and thus they are out-competed by *Cebus*. A more likely explanation, however, is that their population has been put in check by different predators, not only constrictor snakes and wild cats, but also by capuchin monkeys. To date, all species of *Cebus* have been observed preying upon a range of vertebrates species except other primates (Rose, 1997; Freese and Oppenheimer, 1981), but there is some anecdotal or indirect evidence, at least for *C. apella* and *C. capucinus* that they might prey upon other primate species (Baldwin and Baldwin, 1977; Freese and Oppenheimer, 1981). In an environment like the Caatinga it is possible that *Cebus* could prey upon *Callithrix jacchus*, which fall in the body weight category ($\leq$ 1 kg) of their typical mammalian prey (Janson and Boinski, 1992). Although I never observed a predation event, nor found any remains of marmosets in 77 dungs analysed from at least 6 different groups of *Cebus*, I noted that marmosets were always nervous and fled in silence if a group of *Cebus* approached.

Variation in primate abundance amongst different types of habitats has been linked to inter-specific competition, predation, differences in plant composition and structural heterogeneity of the habitat, hunting pressure, quality of food resources and historical factors (Butynski, 1990; Brugiere *et al.*, 2002; Cullen *et al.* 1999; Emmons, 1984; Janson and Chapman, 1999; Lopes and Ferrari, 2000; Peres, 1997a,b). However, when a primate species such as *Cebus* exhibits similar abundance across a series of habitats, even with great variability in forest structure and food availability,

invariably the most plausible explanation invoked is the 'litany' of generalist food habits (e.g. Bennet *et al.*, 2001; Fragaszy *et al.*, 1990; Wallace *et al.*, 2001).

Unpredictable rainfall pattern in the Caatinga might produce severe alterations in the primate abundance over the long term, since from year to year there is a great variability in the number of trees fruiting and during *El niño* years, droughts are severe. It is reasonable to assume that *Cebus* is better equipped to cope with these contingencies than are marmosets and howlers monkeys. Their larger body size may have allowed them to move efficiently to more favourable areas, but ability to cope does not explain why *Cebus* populations in the Caatinga have a similar group size to populations living in wet forests.

While a generalised diet may explain abundance, this may not be the best justification for similarity in *C. apella* group sizes across different types of habitats. Some authors suggest that the use of palm-nuts during periods of food scarcity is an important factor sustaining capuchin monkeys in general and particularly for *C. apella* (Janson and Boinski, 1992; Peres, 1994a; Spironello, 2001; Terborgh, 1983), but that particular area of Caatinga was practically devoid of palm trees. In over 5,000 ha I could find only 3 palm trees (*Copernicia* sp.).

It can be suggested that *Cebus* might typically live at their ecologically and cognitively tolerable maximum group size (e.g. Dunbar, 1996), which raises interesting questions about their sociality. Could it be that *Cebus* is more constrained socially by resources than are Old World cercopithecoids? And if this is so, there may be implications for social intelligence. I will return to these issues in Chapters VI and VII

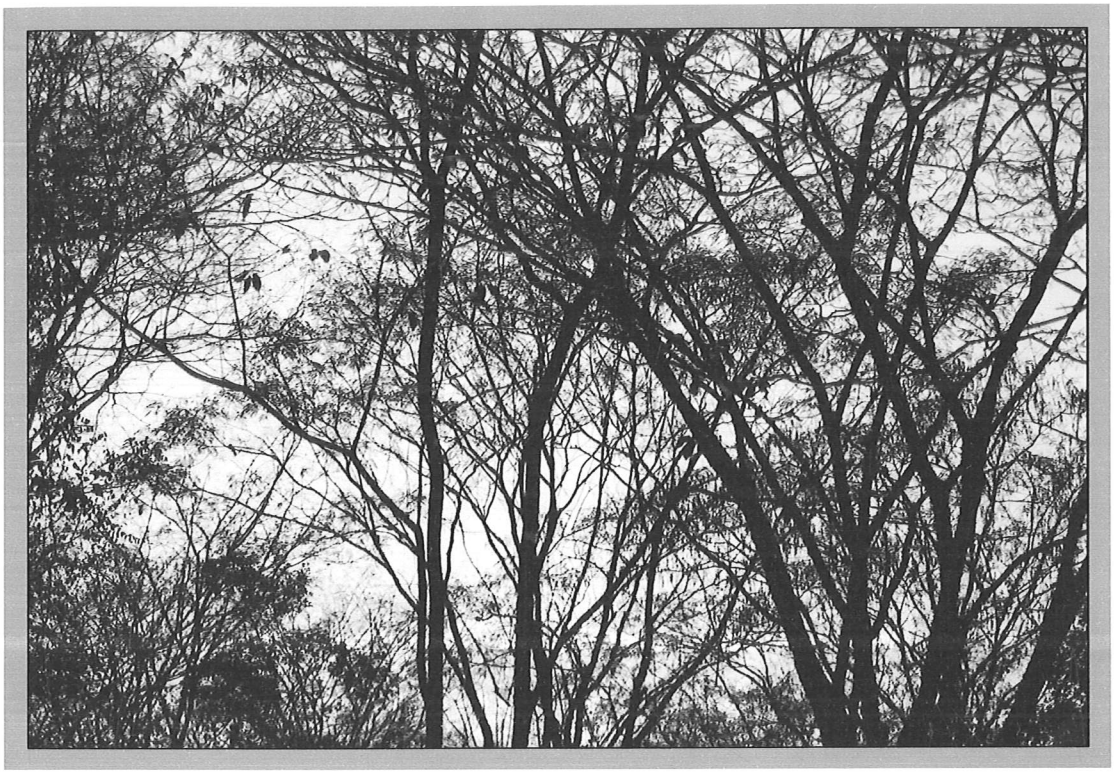
Furthermore, although the density of *Cebus* for the area is low, even considering the limitation of the regression and its probable overestimation, it is

nonetheless similar to the densities observed in some areas of the Atlantic forest and Amazonia (Chiarello, 1999, 2000; Peres, 1997a; Cullen *et al.*, 2001). Why does *Cebus* in this harsh area occur at a relatively similar density to those in areas of rainforest and why is their group size unaffected by the low availability of food? Which strategies allow them to survive there? It is likely that their capability to thrive in the Caatinga dry forest is a consequence of their destructive foraging technique and also a function of their cognitive abilities. I will analyse these possibilities in the next chapters.

SUMMARY

- Each of the sampled habitat types (Canyons, Plateau and the Cliffs) had an individual pattern of mammal abundance and diversity, and the environmental features of these habitats were the main factor explaining the mammal abundance. Canyons were the habitat with the highest number of mammals species encountered and the relative abundance of mammals there was higher than in the other sampled areas. Mammal abundance in the Plateau was extremely low and this can be linked with the harsher conditions of the Plateau. Cliffs were intermediate in mammal abundance. Over 67% of mammal abundance in the Canyons was due to the rodent *Kerodon rupestris*, while primates account for 82% of the relative mammal abundance along the Cliffs.
- The higher abundance of primates along the Cliffs probably is consequence of its greater heterogeneity in forest composition and structure, potentially increasing the diversity and availability of food resources. Overall the abundance of primates in the Caatinga dry forest is very low and almost certainly this is a consequence of low abundance of food resources both in space and time.
- Among the three primate species found in the area, capuchin and marmosets had the same average encounter rate, while howler monkeys were infrequently

seen. Apparently the harsh condition of the Caatinga had a more deleterious effect on group sizes for howler monkeys and marmosets, which were significantly smaller than in other forest types. Capuchin monkeys, however, had average group size within the range reported for Amazonian and Atlantic forests. Usually, the generalised diet of capuchin monkeys is the explanation most frequently invoked for their abundance in different habitats and for the relative independence of group size from ecological constraints. I suggest, however, that this may not be the best justification for similarity in *C. apella* group sizes across different forest types. Foraging style and cognitive abilities probably are more important factors accounting for these similarities.



Sunrise in the forest.

Chapter V

FORAGING AND FEEDING ECOLOGY: SURVIVING IN A HARSH ENVIRONMENT

INTRODUCTION

Having described the habitats, outlined their productivity and assessed how these influence the density of mammals, I will now focus on the *Cebus* in particular.

The basic questions addressed in this chapter are the following:

- How do the capuchin monkeys survive in the harsh dry environment?
- What are the specific strategies in foraging, ranging or behaviour, which allow them to cope with seasonal extremes of low food availability and abundance?

Most species of primates living in seasonal habitats tend to switch their food types to alternative resources and/or use behavioural strategies to enhance food acquisition and reduce energy expenditure during times of food shortage (Peres, 1994a; Terborgh, 1983; Clutton-Brock, 1977).

In a long-term study of a forest primate community at Lopé, Gabon, Tutin *et al.* (1997) observed that, during the dry season when fruits are scarce, the diet of all eight primate species studied shifted to include more non-fruit foods, and some less preferred food items were eaten only when fruit was scarce. In a primate community in Amazonian forest, Terborgh (1983) provides striking examples of seasonal changes in diet and home range. Five monkeys species studied showed an increase in home range size and shifted their diet during times of food scarcity. For example, during the dry season *Cebus apella* and *C. albifrons* increased their home range and spent more time feeding on palm nuts and insects, but palm nuts were much more important to

C. apella than to *C. albifrons*. Other Neotropical primates, such as tamarins and marmosets, also increase their home range size as well as day range, but they switch their diet from the less available fruits either to nectar or gum (Ferrari and Lopes-Ferrari, 1989; Alonso and Languth, 1989). Other species such as *Alouatta paliatta* and *Ateles geoffroyi,* form sub-groups when food patches are depleted, which enables a better use of a large number of dispersed, small food patches and also minimises travel cost and feeding competition (Chapman, 1990). All these changes in foraging strategies are part of the primates' attempts to maintain a positive balance between energy intake and expenditure.

Seasonal food shortage and primate responses

In highly-seasonal habitats, primates exhibit marked changes in feeding behaviour. For instance, Brown and Zunino (1990) showed that *C. apella,* living in a habitat with a great seasonal variation in fruit availability, overcame the seasonal fruit scarcity by increasing the consumption of leaves and even including bromeliad leaves in their diet, a resource not used by other primates. In the dry forest of *llanos*, Venezuela, the only fruit in the diet of *C. olivaceus* during the dry season was the hard fruit of *Guazuma* and, during this food bottleneck period, invertebrate foraging and feeding on roots were much more important than they were in the wet season (Robinson, 1986). Even in wet forest, seasonal food shortages can occur: insect resources seem to be an important resource during lean food times for *Cebus* (Oppenhaimer, 1982).

Although seasonal changes in food supply occur to a greater or lesser extent in all environments inhabited by primates, these tend to be more marked in dry habitats, where plants concentrate flowering and fruiting around the beginning of rainy season

(e.g.: Oates, 1987; van Schaik et al., 1993). Thus, in a seasonal dry forest, food shortage is predicted to have more drastic effects on the life of a primate than in the tropical rainforest. Moreover, primates living in forests with a low diversity of trees, such as dry forests in general, probably face more frequent and longer periods of food scarcity since a higher richness of trees species can be viewed as providing a fall-back during food-lean times (Chapman *et al.*, 1999).

In tropical forests, keystone plant species are thought to exist; i.e. plants that are important for the animal community due to production of edible food throughout times of food shortage (van Schaik *et al.*, 1993). Studies in wet forests, e.g. Amazonia forest, have shown that during times of food scarcity capuchin monkeys change their diet to less preferred food item or rely on keystone resources (Terborgh, 1983). However, the presence of keystone species seems to be lacking in some habitats. For instance, Tutin *el al.* (1997) did not find a keystone plant species or genus for any of the primates at Lopé, Gabon, while in another African rainforest in Cameroon, Yamakoshi (1998) registered two species as keystone resources used by chimpanzees. Keystone species apparently are more important in drier habitats, where their disappearance can force a primate group into extinction (e.g. Lee and Hauser, 1998).

The Caatinga forest and its ecological constraint

In the Caatinga forest, finding food might be a more difficult task than is the case in other types of dry tropical forests. Even during the wet season, the patterns of fruiting seem to be quite stochastic. Depending on the amount of rain, some plant species fail to fruit or may show complex and unpredictable fruiting patterns (Chapter III; Machado *et al.*, 1997). Thus, the characteristic climatic pattern of the Caatinga

(as delineated previously in Chapter III), coupled with idiosyncratic fruiting patterns could mean that resource scarcity exists for the primates for long and unpredictable periods. How does *C. apella* cope with these constraints? How can *C. apella* survive in such a harsh environment? Is there a keystone species (or several) that allows capuchins to survive during the drought?

As noted above, the most frequent solutions to cope with food scarcity are expansion of the home range and switching the diet to alternative foods (Clutton-Brock, 1977; Peres, 1994a). However, during times of food scarcity *Cebus* spp. tend to increase time spent foraging on insects (Chapman, 1990; Robinson, 1986) and when foraging for insects the members of group spread out widely (Freese and Oppenheimer, 1981).

Animal prey (invertebrate and vertebrate) is thus a particularly important food source for *Cebus* and invertebrates seem to constitute the greater bulk of their total protein intake (Janson and Boinski, 1992). In a dry habitat, however, invertebrate prey such as insects are more abundant during the rainy season (Miller, 1996; Poulin *et al.*, 1992; Robinson, 1986). One important class of prey for capuchin monkeys are those insects hidden (embedded) in the substrate (for instance beetle larvae, wasps and bees, ants nests etc), which require the use of force to expose them (Janson and Boinski, 1992). Terborgh (1983) observing the high frequency with which capuchins, mainly *C. apella*, engaged in biting open bamboo and branches, and the striping of bark from dead trees and branches, coined the term 'destructive foraging' for these type of activities. This is one of the most marked features of the feeding ecology of capuchin monkeys, and gives them access to resources that are inaccessible to most species of primates. These embedded prey resources, such as wood-boring insect larvae, live inside dead branches where the environmental conditions could be more amenable

and thus they are probably less seasonally available, representing a reliable food resource throughout the year, while the abundance of other open air invertebrates may fluctuate.

If different types of foraging give access to diverse type of prey, then changes in prey consumption will happen in accord with the season and with the availability of different invertebrate prey.

Sex differences in foraging, either in terms of time spent or in the types of foods consumed, are another aspect likely to be influenced by environmental factors. The differential use of resources and microhabitats by males and females, and by young animals (e.g.: Fragaszy, 1986, 1990), could reduce levels of individual food competition. Therefore, it is plausible to suggest that greater age and sex differences in foraging and microhabitat use will exist for *C. apella* in the Caatinga by contrast to wetter forests. *C. apella* also shows sexual dimorphism in body size, with males being larger than females. The males also possess larger infratemporal fossae associated with larger masticatory musculature than do females (Masterson, 1997). These features could allow males access to resources with which females and younger animals could not physically cope. For instance, Robinson (1986) observed that sometimes individuals of *C. olivaceus,* chiefly the adult males, uprooted saplings of up to two metres in height in order to eat their roots, and that this resource was particularly important during dry season. This raises the possibility that adult females and juveniles could take advantage of the male strength to obtain food remains during periods of scarcity.

Age-sex class differences in use of space and foraging activities

In all of the species of *Cebus* studied so far, the sexes differ markedly in the use of space and time spent foraging; males use the ground significantly more than do females and juveniles and tend to spend much less time foraging than do females (Robinson, 1986; Fragaszy, 1990). These differences could be seen as a behavioural strategy to reduce feeding competition, which might be more marked in dry areas. As an explanation for these differences, however, Fragaszy (1990) suggested that there was a disadvantage to females of foraging on the ground where the risk of predation is higher (Robinson, 1986; Rose, 1994) and, since males are larger (they also have absolutely greater foraging requirements, although they should also be more energy efficient) they may be less vulnerable to predation and thus are able to take more risks. More recently, Rose (1994) suggested that males simply have a higher foraging return on the ground, i.e. males caught up to 31% of larger invertebrate on ground and success rate increased with amount of time spent on the ground, and she dismisses any ecological explanation for sex differences in foraging or use of space. This 'niche' separation between the sexes could reduce feeding/foraging competition. If feeding/foraging competition is driving differential use of space or resources by males and females, then such differential use of space or types of foraging should also be more pronounced in drier habitats, where the low availability of food would exacerbate sex differences.

The ecological constraints faced by *C. apella* living in Caatinga forest are not limited to those of food scarcity, but also include an increased vulnerability to predation. During the height of the droughts, almost all trees lose their leaves and thus the forest becomes more open, increasing the potential predation risk. In the dry forest

of Llanos, Venezuela, *C. olivaceus* during the dry season spend more time on the ground, even though the risk of predation is higher (Robinson, 1986; de Ruiter, 1986). Chapman (1986) observed predation of a wild *C. capucinus* by a boa snake (*Boa constrictor*) during the dry season and argued that predation seemed to be more frequent during dry season when the capuchins spent much more time on the ground, hence becoming more vulnerable. Thus, *C. apella* should reduce the time spent in feeding activities and spend more time performing vigilance behaviour during the drought in order to reduce predation risk.

Aims:

The aims in this chapter are to describe the foraging behaviour of individuals in one group of *Cebus apella* in relation to:

- Seasonal changes in food abundance
- Age-sex differences in resource use
- The use of embedded foods

Finally, I will describe tool use as a mechanism for the extraction of hidden resources as this is a behaviour unique to this population of *Cebus*.

METHODS

Study group for foraging and activity budget observations

In October 2000 I started to habituate and follow a group of *Cebus apella libidinosus* composed of 5 individuals (one adult male, 3 adult female and an infant-juvenile male). In this group only the adult male (Lampiao) was wild, the others came from captive settings and had been released in the area by the IBAMA and the Park managers in July-August 2000. On 24 of December 2000 at 14:05 h a second group (two adult males, two adult females and one juvenile male and one juvenile female) appeared in the provisioning area and engaged in agonistic interactions with the resident group. These agonistic interactions consisted mainly of calls and chasing high in the canopy (making it difficult to identify the performers) and were done primarily by the adult males. After about two hours, the invading group left the area. On the next day, this wild group entered the area again and agonistic interactions again occurred. On this occasion, one of the captive females (Peta) supported the male Lampiao during the encounter against the other group. When the wild group left the area, after 20 minutes, I perceived that Peta had a perforation on her left foot probably caused by a bite by a monkey from the other group. By the 18 January 2001, the 'captive' females were moving together with the wild group. Some aggression and agonistic interactions towards the 'captive' females were still taking place. On one occasion, all the individuals of the wild group attacked one of the 'captive' females (Clarinha), who fled. This invading group apparently evicted (or killed) Lampiao, taking over the area as well as the resident adult females. The new alpha male (Boludo) was lacking hair and had scars on his shoulders and back. The 'captive'

individuals mingled successfully with the wild group, forming a stable group with 10 individuals (Oitenta group). I observed this group systematically until January 2002 with additional observations in February and March 2002. The data I present here cover the period of Jan-Dec. 2001. During this time the group was socially stable with only minor changes in composition. In November 2001, one adult male left the group and in December two 'captive' females died (Table 11 for details).

Table 11. Details of group composition during the study. A= adult; J= Juvenile; m= male; f= female

Individual	Age/Sex	Source and observations
Lampiao	A/m	Wild; alpha male disappeared in Jan. 2001
Peta	A/f	Captive; with infant on 21/03/01 killed (?) in the same week. This female disappeared (died?) in Dec. 2001
Desc.	A/f	Captive, dead(?) Dec. 2001
Clarinha	A/f	Captive, had an infant in 26/11/01 killed by the alpha male on this date.
Juv.	J/m	Captive
Boludo	A/m	Wild; alpha male
Wfemale	A/f	Wild; had infant in November 2001
Cara-Branca	A/f	Wild; had infant in November 2001
Adt	A/m	Wild; joined another group November 2001
Charlotte	J/f	Wild
Juv.II	J/m	Wild

The group was provisioned by the direction of the park (maize, manihot or cassava and sometimes fruits and sunflower seeds) and consequently spent much of their time around the provisioned area. In February 2001, I asked the personnel responsible for giving food to stop provisioning and, probably as a consequence, the group disappeared from the area for about two weeks. The provisioning continued again from March, but as this month had higher fruit availability I asked for the provisioning to be kept at a minimum. Unfortunately, I was only in the monkeys' area for 2 weeks each month (due to the population and vegetation surveys elsewhere in the Park – see Chapter III and IV) and it is likely that the monkeys were given more

food when I was away from the area. Sometimes it was impossible to control the amount of food given to the monkeys. During the dry season, the bulk of the food provided to the monkeys consisted of maize (about 50-70 corns) and dry manihot tubers (about 10 kg) placed in the provision area once a month. The group spent over 50% of their time around the provision area.

For estimating home range I took the group's position using a GPS. Unluckily I did not own the equipment and thus on many occasions I just tagged the group's position in the field and returned later with the GPS to take the co-ordinates. I inserted the collected GPS points into the ArcView program and estimated the home range by linking the extreme points and then calculating the smallest area that had most of the GPS points. This form of minimum polygon range estimate (Harris *et al.*, 1990) was all that was possible given the paucity of data points available for range size calculations. The group used an area of about 135-140 ha.

Sampling

The most frequent sampling method used in studies of *Cebus* ecology is the continuous focal-animal sampling (e.g. Chapman and Fedigan, 1990; Rose and Fedigan, 1995). However, Fragaszy *et al.* (1992), comparing focal-animal and group - scan methods stressed some problem with the focal-sampling method, especially the costs of limitations in data collection; for instance, during focal-animal sampling a single subject must be found and kept in view for a certain amount of time requiring the full attention by the observer, who thus can miss interesting events or interactions on the part of other individuals in the group. Moreover, they argued that the scan sampling permits the collection of a larger amount of useful data than animal focal sample for the same amount of observation time. As a final recommendation,

Fragaszy *et al.* (1992) suggest the use of a mixed sampling containing both focal animal and scan sampling.

Data collection for activity budgets and feeding:

I followed a method as delineated by Robinson (1986) and Miller (1996), who also observed capuchin monkeys living in a dry habitat. I observed the group using slow scan sampling at each half-hour. Usually it took an average (±SD) of 16.56 ±7.2 min to locate most of the individuals in the group (median 15.5 min) (Fig. 22).

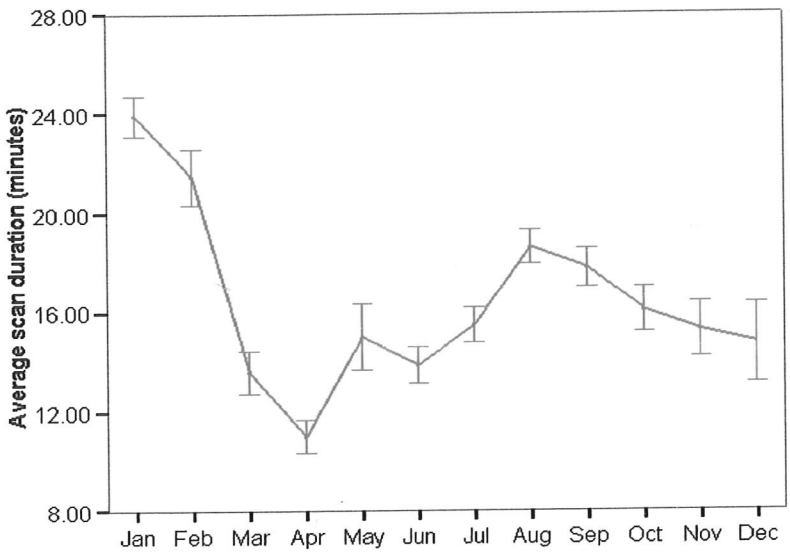


Figure 22. Mean monthly scan duration. Error bars show standard error of the mean.

The long interval between scans has the advantage of avoiding dependence between successive scans on the same individuals. When I located an individual, I recorded only the first observed behaviour that lasted a minimum of five seconds. During the scans I tried to locate all animals, but in most of scans I was able to find only 70% of the group (median = 7). The average number (±SD) of individuals in a

scan was 7.3 ±1.4 and on many occasions part of the group was in the trees while the others were on the top of rocky outcrops in the canyons that were out of view. As the topography was quite rugged, with many outcrops, it was common to see only part of the group, while the remainder was out of view. In January, particularly, it was extremely hard to locate and follow the group, because they were still not well habituated to my presence, but from February onwards the number of individuals in the scan increased and the time spent locating individuals was reduced (Fig. 23). I followed the group from dawn to dusk, but on many occasions I could locate the monkeys only in the middle of morning and at other times I lost the group for the remainder of the day. I followed the group for an average of 5.7 days mo^{-1} (range 3 to 7 days mo^{-1}, mode 7 days). I collected 614 scans comprising a total of 307 hours in over 390 contact hours (see Appendix 6).

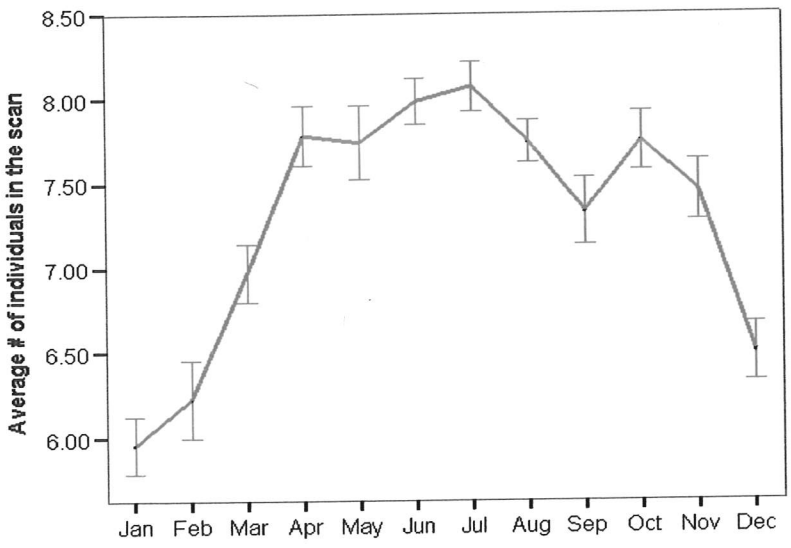


Figure 23. Monthly number of individuals in the scan. Error bars show standard error of the mean.The decrease in December and November was due to emigration of one adult male and the probable death of two females (see Table 11).

In addition to the scans I also used both continuous and one-minute interval focal animal sampling in 10-min. sessions. These focal samples were made on different adult individuals when they were visible. The number of focal samples/individual varied from 23 to 37 with a median of 24 focals each. The focals occurred interspersed with the scan samples. The total hours of focal samples were very low and I used these data only in analyses of specific questions (e.g. frequency of eating or success in foraging). For the activity budget and analyses of behaviour by age-sex classes I used data gathered through scan samples.

During focal and scan samples, I recorded the following activities: **foraging** (looking for animal prey in different substrata or using strenuous physical activity to remove a plant part, for example a root, for eating), **feeding** (gathering and ingesting plant material or eating animals), **moving** (either sustained travel or short distance movements on the ground or climbing in the trees or rocks), **social behaviour** (distinguished as grooming, aggression, play), **vigilance** (looking at the sky or around at areas beyond the immediate substrate), and **others** (drinking, lone play, self-grooming, copulating, approach etc). All of these behaviours are similarly defined in diverse studies on ecology of *Cebus* spp. (e.g. Robinson, 1986; Rose, 2000; Terborgh, 1983). Another behaviour I recorded was tool use, the most accepted definition of this behaviour is that of Beck (1980): "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object...". In this thesis, following van Schaik *et al.* (1999), I applied this definition to tools used in the context of foraging (details in Chapter VI).

All occurrences and *ad libitum* observations were used to register food sharing, copulation, intergroup encounters, tool use, coalitions, scent marking and other rare events. Nearest-neighbour was recorded for each scanned individual in

order to determine patterns of proximity. During focal samples, nearest-neighbour and distance were recorded at each minute.

Foraging and activity budgets

I divided foraging activity into four categories: 1-visual: looking at the foliage, vines or other substrates when searching for animal prey; 2- manipulative: using the hands to "sieve" leaf litter accumulation on the ground or rock outcrops and opening "closed" (rolled-up) leaves searching for hidden insects; 3- destructive: using the teeth and/or hands to break/ tear apart or open twigs and large branches; 4- dig: use the hands for dig. While using tools in a feeding context is also a form of foraging, I decided to treat it as a separate category since no other wild *Cebus* population is known to use tools (see Chapter VI) and also to facilitate comparisons with data on activity budgets from other groups living in different habitats. Nevertheless, for some analyses I incorporate tool use into foraging categories as stated in the results.

During a record of activity I noted the individuals' height, substrate (defined as ground, tree, vines, shrub, outcrop and cliff) and the distance to the nearest monkey during that particular activity. If I had a GPS I took the position of the group at the beginning of the scan. If not, I marked and registered the name of the location in the area and when I could obtain a GPS I went back to these places and took the co-ordinates.

All plant species eaten by the group while it was being followed were identified. I also collected opportunistic feeding data from neighbouring *Cebus* groups and from others groups living in other areas of the Park. In order to have a more complete picture of the diet during times when I was not observing I collected dung of *Cebus* opportunistically throughout the study. A total of 77 dung specimens were

collected. After collection I either dried or preserved the dung in alcohol stored in plastic vials. Some samples collected during the wet season were lost when the seeds present germinated before the dung could be analysed or when vial labels were damaged. All seeds (and other matter) in dung were identified and counted (except for a few dung analysed in-situ, where only seed counts could be made). I could identify most seeds only to genus level.

Evaluation of food resources used by the monkeys

For evaluation of fruit resources, I used vegetation belt transects of different sizes and length, and plots (25 x 25 m) established in different types of habitats (see Chapter III for full details).

In order to evaluate the general abundance and diversity of invertebrates groups I used three methods:

- Pitfall traps, consisting of 12 buried plastic containers in 5 different transects (details in Chapter IV);
- Nest traps that mimic branches used for posture by solitary or semi-social wasps and bees. When foraging, capuchin monkeys break and tear apart branches searching for hidden insects, chiefly Hymenoptera (Janson and Boinski, 1992; Terborgh, 1983). Many Neotropical social, semi-social and solitary wasp and bees make their nest inside dead branches (Roubik, 1989). Thus, opening branches could be another important insect resource for capuchin monkeys. The nest traps used to assess abundance of these Hymenoptera consisted of 3 wooden blocks measuring 30 x 10 x 25 cm with holes drilled to 10-12 cm deep. Each block had between 68 to 100 holes filled with rolled papers and also had two bunches of bamboos (about 10-15 in each group) with different diameters (Fig. 24). The traps were placed in Canyon Esperanca, in the transect bisecting the Plateau and along the Cliffs. At each trap location, I put two sets of blocks separated by distances ranging from 400 to 800 m. I checked the nest traps twice a month (using a probe). When I found a nest, I removed the rolled paper containing the nest and replaced it with fresh paper. I then put the removed paper inside plastic bottles and wait for the brood to emerge to

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identify the insects. The nest traps were established in July 2001 and remained in the field until January 2002.

- Census of insectivorous birds, namely Formicivorae (Antbirds); Picidae (Woodpeckers) and Dendrocolaptidae (Woodcreepers). These birds forage in different ways and occupy distinct niches in the dry forest. For example, Picidae extract embedded insects (Hymenoptera, larvae of coleoptera) from either dead or living branches and tree trunks; the Dendrocolaptidae forage along branches and trunks, looking for insects hidden in the bark or camouflaged on branch and trunk (i.e. Phasmidae, Mantidae; spiders and cockroaches) and finally the Formicivorae forage in the dead foliage on the forest floor or glean the leaves of saplings and bushes looking for caterpillars and other prey. *Cebus* monkeys forage in all of these places and probably compete with these birds for insect resources.

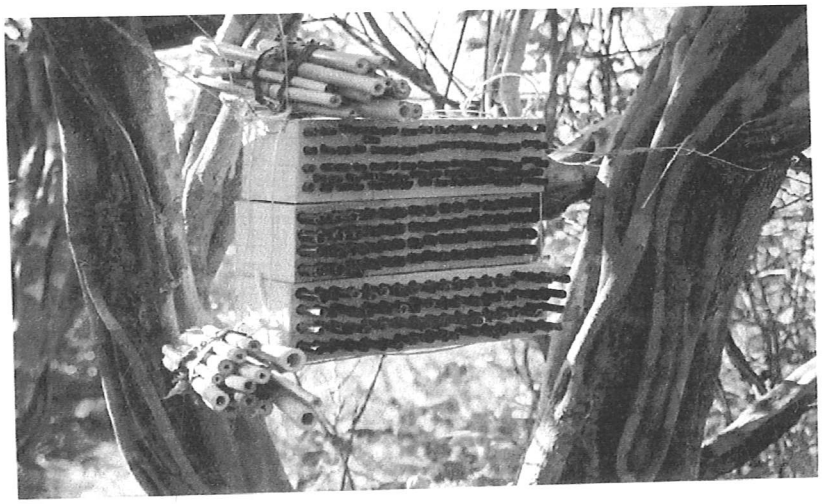

Figure 24. View from the nest trap apparatus, already set up, used for assessing the abundance of bees and wasps in different habitats. This trap was mounted in the Plateau habitat on a *Cenostigma gardnerianum* tree.

I decided to census these insectivorous birds, because I noted, during the census of mammals, that some bird species were almost exclusive to particular type of habitats and that the largest woodpecker species occurred only along the Cliffs, where the monkeys spent most of their time. Thus, this insectivorous guild could be an efficient indirect way to estimate insect population. As such, I used the abundance and

diversity of these birds as a proxy for the variability and diversity of invertebrates in different types of habitat in the Park. The bird census was carried out from February 2002 to September 2002 once a month at random times by the local ornithologist, Lourival Santana. The censuses were done on the same trails as those used for the mammal censuses in the area (see Chapter IV), but these were walked in only one direction (Table 12). During the census, the bird distance to the observer was noted, as was the angle in relation to the trail and distance in the trail, and the forest height used by the birds was also recorded.

Table 12. Details of the transects used for the census of the insectivorous bird guild. The Plateau transec had a total of 7 km, but just 2 km was censused.

Place	Transect length (km)	Total km walked	Habitat type
Baixa Grande	0.9	7.2	Cliff
Jurubeba	0.5	4	Cliff
Baixao da Vaca	1.4	11.2	Canyon
Esperanca	1.6	12.8	Canyon
Zabele	2	16	Plateau

Data analyses

To determine activity budget, I calculated the sum of the different activities for each individual by season and then divided it by the total number of scans for each individual in the specific season (see Chapter II for season definitions). I used these individual values for doing the statistical tests. Before running statistical tests I tested the distribution of the variables as detailed in Chapter II. Most activities conformed to a normal distribution, but I used non-parametric statistics for the majority of tests, since the non-parametric tests are both robust and independent of the assumptions of normality (Martin and Bateson, 1986; Chapter II). In some cases, however, I used parametric statistics due to a lack of appropriate non-parametric test and for its higher

power (i.e. lower probability of incurring a type I error) compared to non-parametric tests. One of the biggest problems was the small sample size of individuals, a plague in behavioural ecology. In order to circumvent this problem, I pooled the data derived from different individuals for some of the analyses, namely when comparing different age-sex classes. Pooling data is problematical since it can give misleading results (reviewed in Martin and Bateson, 1986). However Leger and Didrichsons (1994) show that pooling can provide reliable estimates for the population. Additionally, the statistical results I obtained from the pooled data are backed by similar results in other studies on the ecology and behaviour *Cebus* spp.

RESULTS

Activity budget

Overall, individuals in the group spent an average of 22.3% of time in foraging (mean = 22.9%, including tool use), 19.6% in feeding and 37.1% moving (n= 4,489 activity records). These data exclude feeding or foraging on the provisioned foods. The activity pattern of the individuals was very similar across the seasons (Fig. 25). Moving was the only activity to show a significant increase during the dry season (Wilcoxon test, Z= -2.14; n= 10; p= 0.032) and social activities tended to be more frequent during the wet season (Wilcoxon test, Z= -1.78; n= 10; p= 0.074). Contrary to expectations, vigilance behaviour was more common during the wet season when the individuals were less exposed to predators since leaf cover was higher, but the difference was not significant (Wilcoxon test, Z= -1.58; n= 10; p= 0.11).

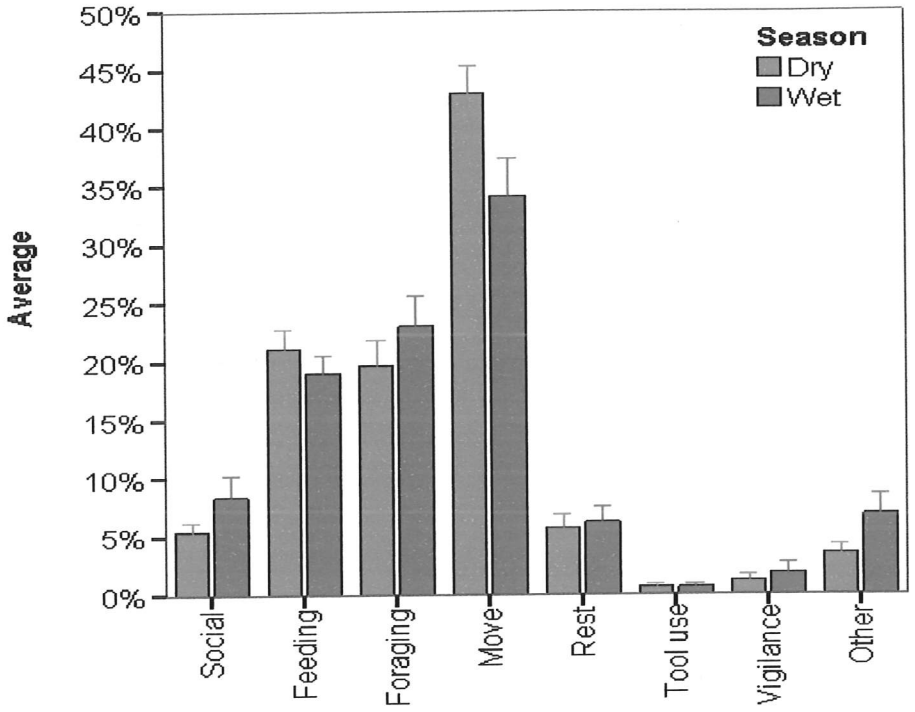

Figure 25. Mean percent (+ SE) of time spent in different activities by season.

The monkeys spent up to 22.5% of their time on the ground (excluding records of feeding on provisioned food), and during the dry season they spent significantly more time on the ground (Fig. 26) (Wilcoxon test, Z= -2.7; n= 10; p< 0.01,). Overall, this population spent much more time on the ground than do other *Cebus* living in dry habitats. For instance, *C. olivaceus* living in the Llanos dry forest spent only 13.4% at a maximum of their time on the ground (Robinson, 1984). The ground was used chiefly for foraging (average 28.6%) and moving (26.3%). The monkeys spend significantly more time in the middle forest strata (4-6m) than at other levels (ANOVA $F_{5, 54}$= 77.9; LSD post hoc test p<0.001).

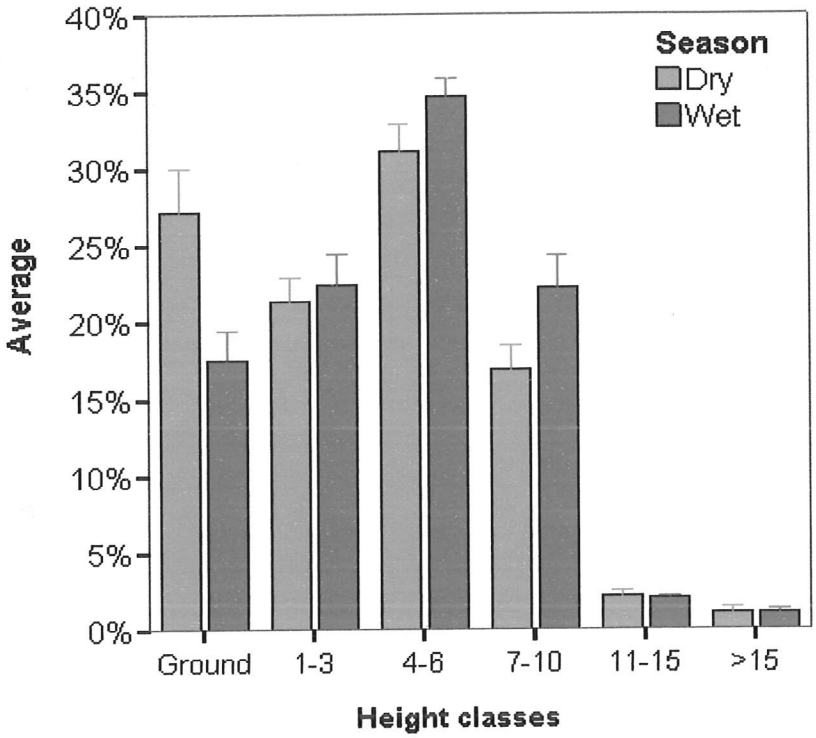

Figure 26. Mean percent (+SE) of scans at different forest height for *C. apella libidinosus* during the two seasons. Note the high preponderance of using the ground in the dry season.

Age-sex classes differences in activity

There were differences in time spent in the various activities between age-sex classes (Fig. 27). There were significant differences among age-sex classes in the amount of time devoted to foraging (Kruskal Wallis ANOVA, H= 13.5; df= 2; p=0.001). Adult females foraged for significantly more time than did any other age-sex classes (Mann-Whitney test $p<0.01$; Bonferroni correction p= 0.025). Juveniles tended to spend somewhat less time feeding did adults (H= 5.7; df= 2; p=0.06). Overall, these differences are similar to findings from studies on other *Cebus* species.

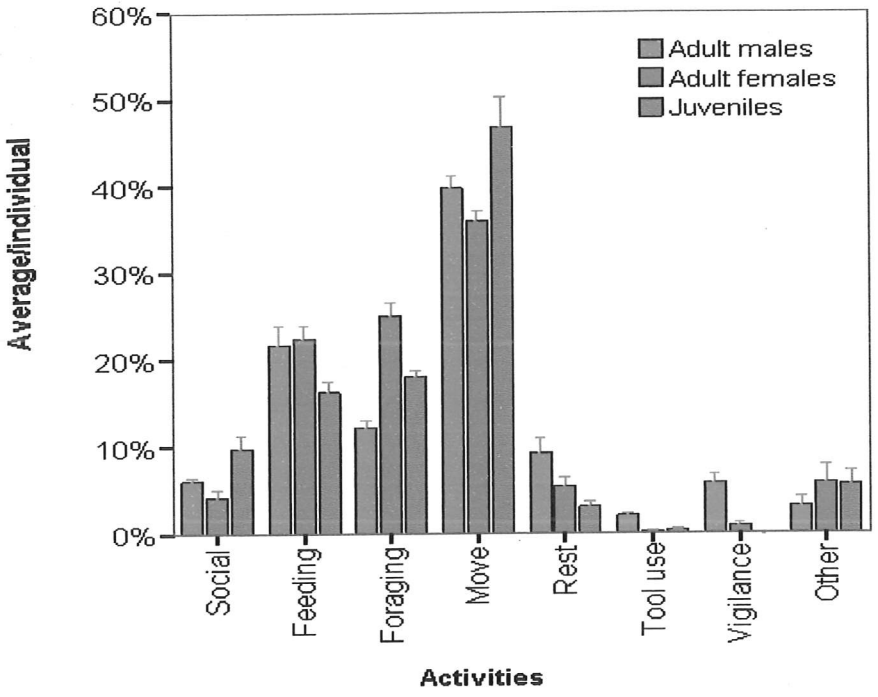

Figure 27. Mean percent (+SE) of time spent in the major activities for the different age sex classes.

The patterns of vigilance and rest were very consistent with findings in *Cebus capucinus, C. albifrons, C. apella* and *C. olivaceus* (Fedigan, 1993; Fragaszy, 1990; Rose, 1994). As has been generally observed, males spend much more time resting and in vigilance than do females. Van Schaik and Noordwijck (1989) highlight that male vigilance enables females to forage more effectively by reducing their time costs of predator detection and maximising their intake.

It is most likely that the individuals obtained the majority of their dietary protein from foraging as much of this was for protein-rich insects (see below). Accordingly, larger individuals such as the adult males should have spent more time foraging, but rather it was the females and juveniles that were spending significantly more time foraging. This discrepancy is noteworthy and raises the possibility that

males could be obtaining larger or more prey returns from their foraging activity. Alternatively, as the smaller females and juveniles have relatively greater energy requirements, they could be forced into spending more time foraging for high energy food items.

Inter-individual distance during different activities

The inter-individual distances, excluding records of feeding on provisioned foods and social activities where the individuals were typically in close proximity, were very similar during the dry ($\bar{x}$= 6.9m; ±SE 0.14; median= 6m, n= 1,871) and wet season ($\bar{x}$= 7.1m; ±SE 0.22; median 5m; n=1,620). There was, however, considerable variation in distance between adult animals, who were often engaged in different activities (Fig. 28). Juveniles were consistently the nearest individuals to adult animals.

Although there was no overall difference in distance between neighbours during the dry and wet seasons, it would be incorrect to assume that the group maintained the same cohesiveness during these seasons. The distances were taken in relation to the nearest individual only and on many occasions, chiefly during the dry season, the group as a whole was much more dispersed, with some individuals more than 50 metres apart. It appeared that two "sub-groups" formed, one of which consisted of the high-ranking individuals plus juveniles and the other composed of the lower-ranking individuals.

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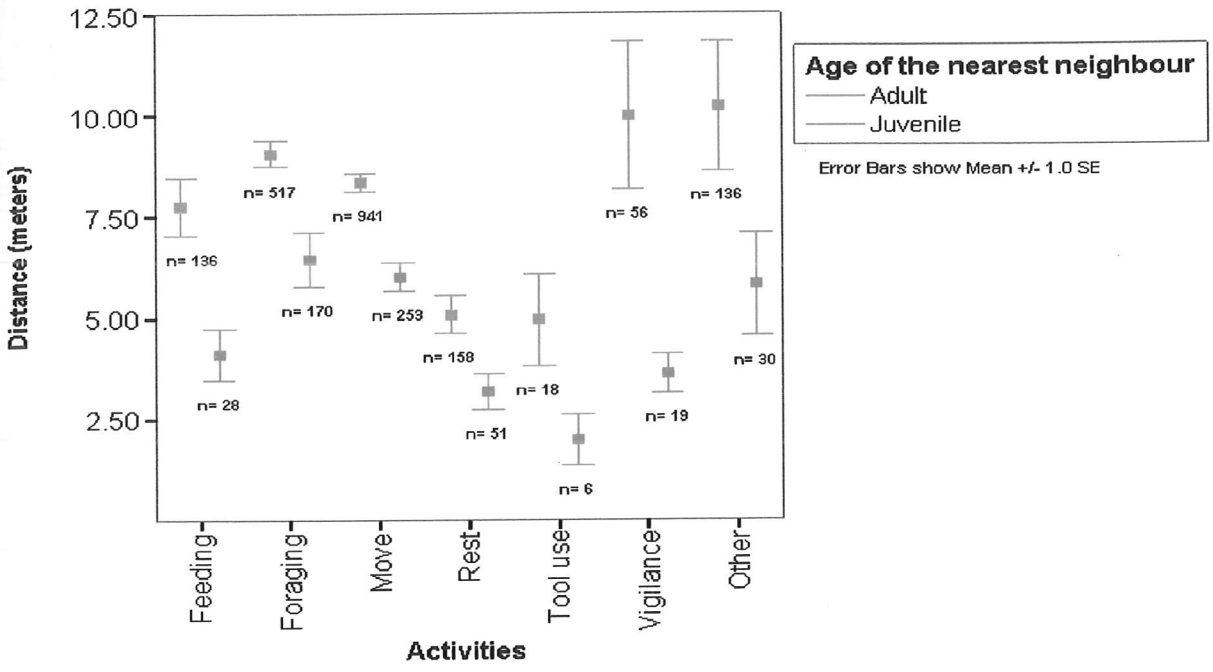

Figure 28. Age of the nearest individuals to adult subjects performing different activities

Foraging

The most frequent types of foraging were visual (48.56%; n= 867 foraging records[1]) and manipulative (31.5%). Destructive and digging foraging were less frequent (16% and 3.8% respectively). The time spent in each type of foraging differed markedly between the seasons. During the wet season, the animals spent significantly more time in visual foraging (Wilcoxon test, Z= -2.39; n=10; p= 0.017) probably reflecting the increase in caterpillars and a higher procurement rate of other invertebrates on the foliage. More energetically demanding foraging types, such as digging and destructive foraging, increased during the dry season. While the time

[1] I recorded a total of 916 foraging episodes, but for 5.3% of these I did not note the type of foraging.

spent in destructive foraging only approaches significance (Wilcoxon test, Z= -1.78; n=10; p= 0.074), the time spent in digging was considerably greater during the dry season (Z= -2.67; n=10; p= 0.008). When I included tool use in the analyses, the time spent in the more intensive foraging types increased significantly in the dry season both for digging (Z= -2.31; n=10; p= 0.021) and destructive foraging (Z= -1.98; n=10; p= 0.047). Usually, the larger and stronger adult males were able to break and open larger dead branches than were the adult females. Manipulative foraging was consistently uniform across the seasons (Z= -0.46; n=10; p= 0.65). The similar proportion of time spent on this activity during the wet and dry seasons suggests that foraging success in those microhabitat was not being affected by season. However, an analysis of the number of insects and other invertebrates caught during focal sampling suggests that the success rate (bugs caught/foraging time) was higher during the wet season ($\bar{x}$= 0.4, ±SE 0.09) than in the dry season ($\bar{x}$= 0.26; ±SE 0.06). The individuals had an overall average success rate of 0.31 ±SE 0.05 invertebrates eaten each minute, which was similar to that reported by Terborgh (1983) of a capture of one invertebrate every two minutes.

The return from foraging activity of the adult individuals was usually higher during the wet season and the different types of foraging yielded distinct returns (Fig. 29). Returns were assessed as the total frequency of invertebrates eaten during foraging activity by each individual divided by the total number of focal minutes spent in foraging. The most profitable foraging activity was visual both during the wet and dry season. The only foraging type to present an increase in the return rate during the dry season was destructive foraging, probably due to the significant increase in the amount of time spent this type of foraging during the dry season (see above). For *C.*

capucinus in the dry forest of Santa Rosa, most of the insects eaten in the dry season originated from destructive foraging (Freese, 1977).

Overall, there is a slight trend for the returns from foraging activities to be higher in the wet season (Wilcoxon test, Z= -1.3; n=7; p= 0.17). These data, however, should be viewed with caution since the total focal sampling time was low; just 32.7 hours for the whole group.

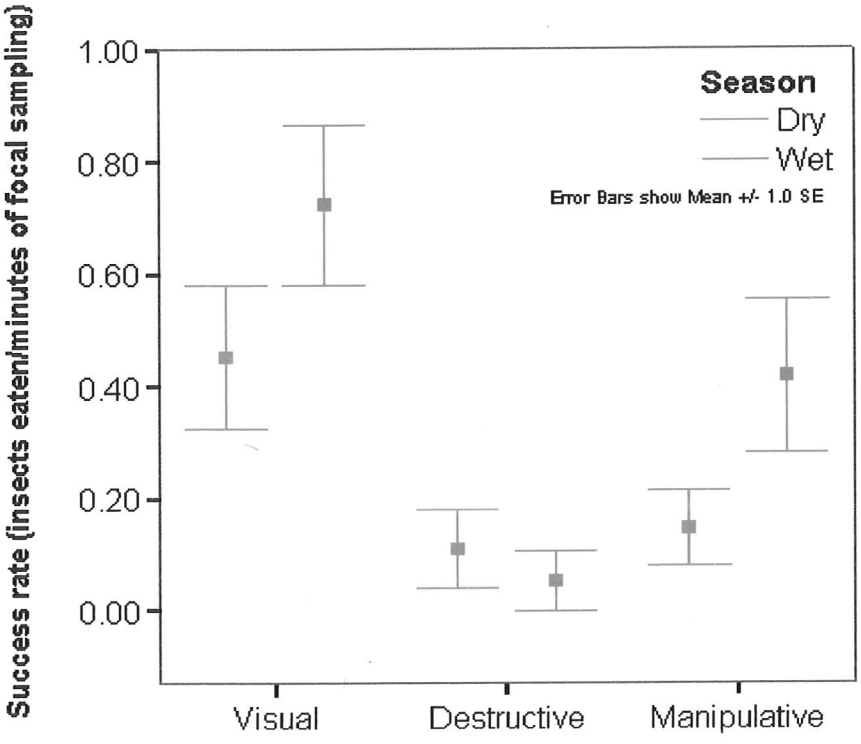

Figure 29. Return from three different types of foraging in each season, measure as the number of insects eaten per minute of focal sampling (success rate could not be calculated for dig).

There are differences in the proportion of time devoted to the four kinds of foraging by each of the age-sex classes. Adult females and juveniles spend most of their foraging time in visual foraging, while adult males concentrate their foraging

efforts on manipulative and destructive foraging (Fig. 30). It is likely that males were obtaining more returns from these types of activities. Fragaszy (1986) observed in *Cebus olivaceus* that males obtained a greater proportion of animal prey items from 'active' foraging (destructive), double the success rate of adult females. Most of the manipulative foraging occurred on the ground and data for *C. capucinus* indicates that the success rate of males at capturing larger prey is proportional to the amount of time they spent on the ground (Rose, 1994).

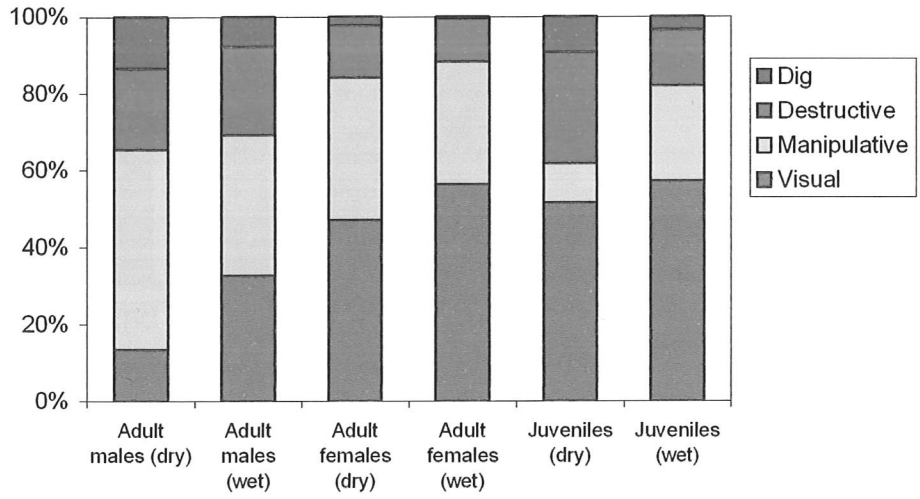

Figure 30. Age-sex class differences in foraging activity by season, proportions were based on absolute values.

These differences in types of foraging employed by the different age-sex classes were reflected in the proportion of time spent at different heights. Adult males spent much more foraging time on the ground (~ 40%) than did any other age-sex classes (Fig. 31). This distinction in use of different heights by adult males and females may indicate some kind of niche separation between the sexes acting to reduce feeding competition. Interestingly, the majority of individuals chiefly used the middle stratum of the forest for foraging (Figure 31 and see Figure 26). Similarly,

other *Cebus* populations living in wet forests, with canopy height twice as tall that of the Caatinga dry forest, also chiefly use the forest middle storey (e.g. Terborgh, 1983). This maybe a behavioural strategy to avoid predation by large raptorial birds.

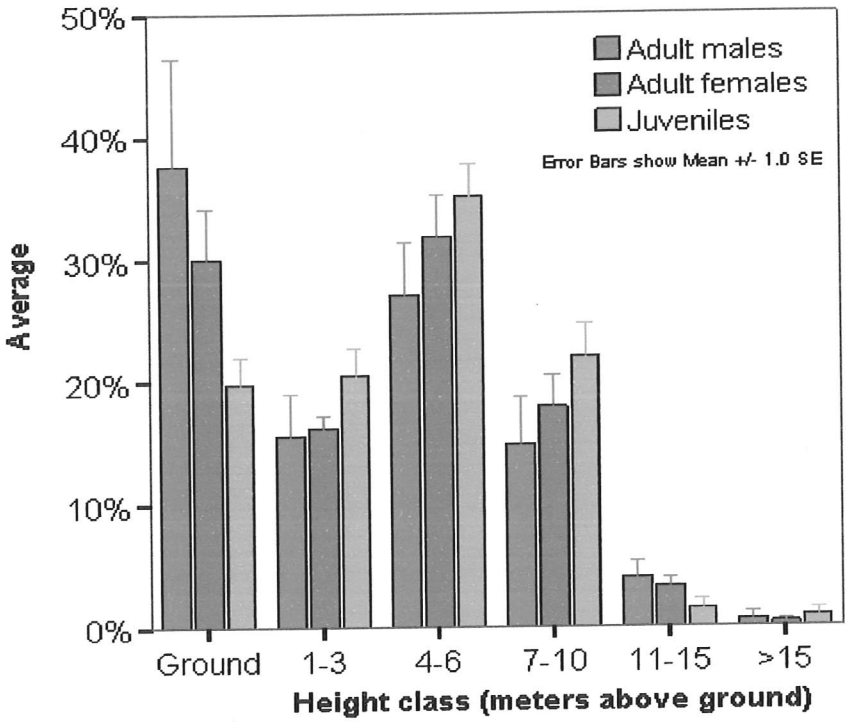

Figure 31. Spatial distribution of different age-sex classes during foraging.

Whilst foraging, the monkeys tended to keep apart from each other, except during digging foraging when their inter-individual distance was significantly reduced ($F_{3, 863}$= 4.6; LSD post hoc test $p<0.002$). It is possible that the smaller distance between neighbours during digging might be a consequence of the clumped distribution of the tubers/roots on which the monkeys were foraging, but it does not rule out the possibility that a closer proximity could allowed some individuals, especially females and juveniles, to 'scrounge' food remains (see Chapter tool use).

I hypothesised that, during more difficult foraging tasks, adult males would obtain larger prey and other individuals in the group could be attracted to the site of

the male's foraging in order to obtain possible food remains. This is a difficult hypothesis to test, and changes in inter-individual distances may provide some evidence in its favour. Indeed, there was a significant difference in distance to nearest neighbour as a function of the sex of the adult animal performing destructive foraging. Other group members were found significantly closer to adult males than to adult females during destructive foraging (Mann-Whitney U= 490.5; n_1 = 23, n_2= 68; p< 0.01). This could suggest that the food found by adult males is larger and other individuals may approach the male in order to obtain food remains or to explore the 'patch' exposed by the adult male. Although monkeys in the group also were found somewhat closer to adult males than to adult females during digging, the difference was not significant (Mann-Whitney test, U= 29; n_1 = 8, n_2= 11; p= 0.2). The only type of foraging without any effect of sex on the proximity to other group members was visual foraging (Fig. 32).

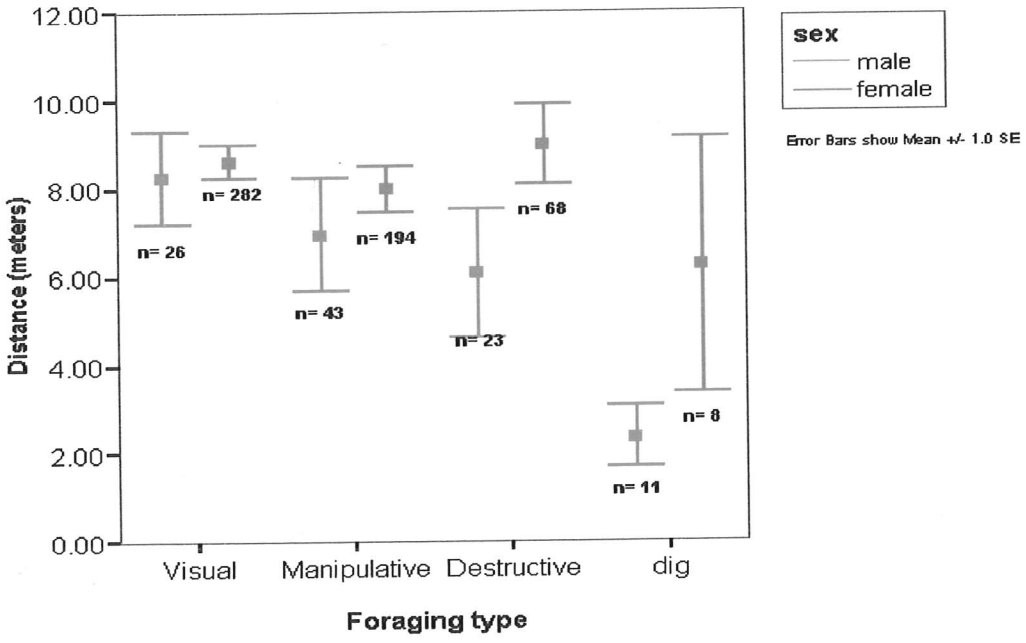

Figure 31. Foraging types performed by adult males and females and average distance of other group individuals to them.

Feeding

This group was provisioned, and consequently most records of food type (77.5%, n= 924) were on provisioned foods (Fig. 33). During the dry season, the monkeys spent significantly more time eating provisioned food (Wilcoxon test Z= -2.29; n=10; p= 0.022), an indirect indicator of the food or energy bottleneck they experience during this season. Nevertheless, despite provisioning the monkeys made extensive use of other food resources. Thus, for further analyses I removed the values of feeding on provisioned food.

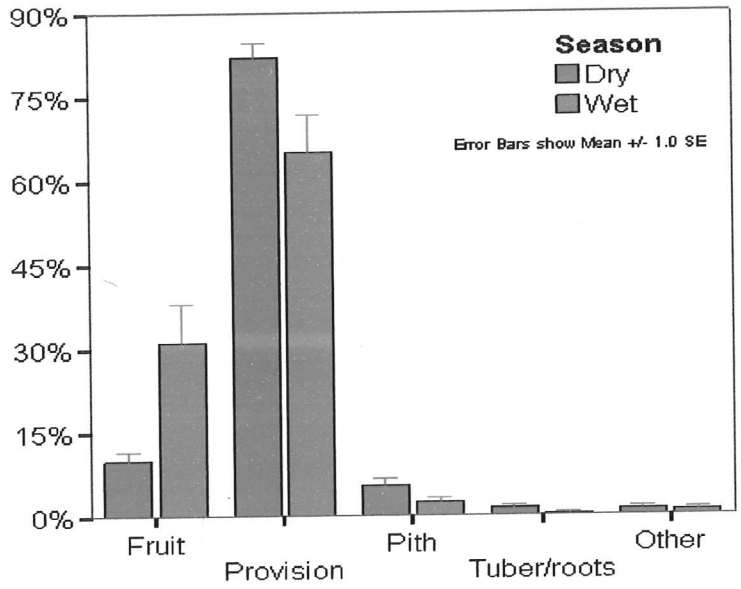

Figure 33. Mean time spent feeding on different types of food by season (n= 924 feeding records).

During the wet season, with a greater number of species fruiting, the monkeys consumed significantly more fruit (Wilcoxon test, Z= -2.8; n=10 p= 0.005). The fruits most consumed in the wet season were from the tree *Zizyphos joazeiro* and from *Erithroxylum* spp., which accounted for 38.7% and 21.5% of the feeding records (n=

116). As I used a slow scan, recording only the first behaviour of an individual, the values of feeding could be underestimated. For example, an individual could switch to another fruit species in the same scan and then spend more time eating the second fruit species by comparison to the first observed species. Since the interval between the scans was long, the effect of such differences might be underestimated. However, analyses of dung from Oitenta group indicate that the values derived from scans are reliable. The most important fruit seeds found in 52 dungs from Oitenta group were *Ficus gomellera* (21.15%); *Copaifera* cf *langsdorfii* (11.5%); an unidentified species (17.3%); *Z. joazeiro* (17.3%) and *Erythroxilum* spp. (9.5%). The availability of fleshy fruits in the wet season was of short duration and the most important fruit sources were consumed for less then 2 months (Table 1). Also the proportion of the four most consumed fruiting trees (above 3% of the feeding scans) bearing fruits was low and limited in time (Fig. 34) indicating the paucity of fruit availability in the area (see Chapter III). A full list of the species eaten is given in Appendix 5.

There were very few species of trees fruiting during the dry season and most of them had wind-dispersed fruits (Chapter III). Fig trees were one of the few species producing fruit in the harsh dry season. Although scans showed a low frequency of monkeys eating fig fruits (2.9% of all the feeding records, n=206), figs were an important dietary item; over 21% of dung from Oitenta group containing fig seeds (17.1% including dung from 6 different groups, n= 77). I monitored the fruiting cycle of 21 *Ficus gomellera* trees in different habitats; a monthly average of 10.31% ±SE 1.91 tree were fruiting in the dry season against 5.5% ±SE 1.91 during the wet season. Due to the *Ficus* spp. asynchronous fruiting pattern, which leads to an almost constant availability of fruit from one individual or another, it may have been a 'keystone' species for the primates in the area.

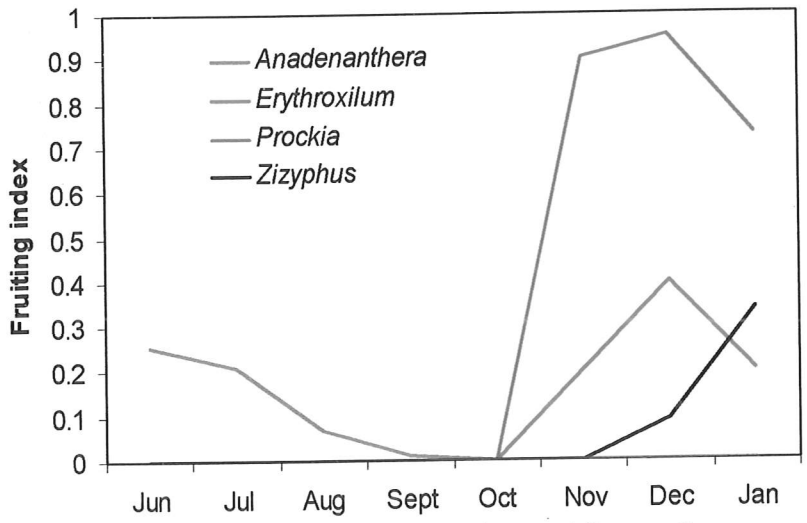

Figure 34. Availability of the four fruit species most frequently consumed by the monkeys. The data for *Zizyphus* originates from phenology of trees in the Canyons II, about 20 km from the monkeys area; in the home-range of the capuchin group this tree in the vegetation plots did not fruit, although trees just 10 meters away fruited copiously. *Trichilia* sp. was not included because it failed to fruit during the phenological sampling period (see Chapter III). The fruiting index was calculated as # of trees fruiting/ total # of trees.

Of the 14 fruit species eaten by the monkeys (see Table 1) 11 were fleshy, two were seeds with aril (*Capparis flexuosa* and *Copaifera* cf. *langsdorfii*) and just one was a dry fruit. Most of the fleshy fruits were consumed during the wet season while figs and a Myrtaceae fruit were the only fleshy fruits observed to be consumed in the dry season. During the dry season, the dry pod of *A. colubrina* was frequently eaten (48.9% of the feeding records for the dry season, n= 90). I was unable, however, to determine if the monkeys were acting as seed predators, eating some part of the coat or searching for insect larvae inside the legume. Another important fruit tree for the monkeys in the dry season was *Copaifera* sp. Although I never directly observed the study group eating its fruit, this species seemed to be a very valuable resource for the first two months of the dry season (May-June), when I frequently found its seeds in the dung of Oitenta group and also in dung from other groups.

The monkeys in this area exploited 26 species for fruit and other plant parts (Table 13), but only nine species accounted for 83.8% of all feeding records (fruit and pith) and just five tree species were responsible for 69.2% of the fruit eaten by the monkeys in the feeding records (n= 206). There was no correlation between density of trees and their importance as a food resource (Pearson's r= -0.3; n=9; p>0.4), indicating that variables other than density were affecting feeding on a particular species. The diet of the monkeys was further constrained by the low diversity of fruiting trees and low proportion of them producing fruits at any one time. Moreover, from year to year there seems to be a great variability in number and species of trees producing fruits. For instance, the rainy season of 2000-2001 was relatively normal and there was a massive fruit production of *Eugenia* spp., *Erythroxilum* spp, *Zizyphus joazeiro* and a *Trichilia* sp. (Chapter III). I used to see the fruits of these species rotting on the forest floor, chiefly inside the canyons, but the rainy season of 2001-2002 was quite unusual with low and patchy rainfall (Chapter II); consequently, the fruit production was lower and some species did not fruit at all.

The low diversity of tree species in the *Caatinga* dry forest, particularly of the species producing fleshy fruit, and the low availability of fruiting trees at a single point in time (Fig. 34) could greatly restrict the availability of food resources. Even considering opportunistic observations from other *Cebus* groups and dung analyses, the list of plants used as food resource was still low, circa 40 species (Appendix 5). In other dry forests, for instance the Venezuelan Llanos, capuchin monkeys use more than 60 species of plant as food resources (Robinson, 1986). Thus, for the monkeys living in the Caatinga, foods that act as alternatives to fruits are of ultimate importance, especially during the dry season.

Table 13. Plants species consumed and seed dispersed by Oitenta group. Life form:T= tree; H= herb; C= cactus; G= grass. Part eaten: P= pith; F= fruit; Fl= flower; T= tuber. The density of trees refers only to vegetation plots (1.2 ha) scattered in the main area where Oitenta group lived.

Species	Life form	Trees/ha	Part eaten	Average percent in the feeding scans	Percent of dung with seeds[a]	No of months the fruit was eaten[b]
Anadenanthera colubrina	T	81.6	P; F	21.1		3
Caesalpinia bracteosa	T	15	P	.42		
Capparis flexuosa	T	13.3	P;F; FL	.99		1
Cereus jamacaru	C	5	P	.77		
Copaifera cf. langsdorfii	T	5	F	--	11.5	
Enterolobium cf contortisiliquum	T	1.6	P	7.2		
Eremanthus martii	H	--	P	2.1		
Erythroxylum spp.	T	50.8	F	11.99	9.5	2
Eugenia sp.1	T	140	F	--	7.7	1
Ficus gomelleira	T	2.5	F	2.7	21.15	3
Ipomeia sp.	V	--	T	--		
Laseis sp*.	G	--	S	.42	1.9	1
Miracroduon urundeuva	T	3.3	P	.3		
Myrtaceae	T	3.3	F	.625	5.8	1
Pilosocereus piauhyensis	C	--	P	--		
Pouteria sp.1	T	3.3	P; F?	.38		
Prockia crucis	T	19.1	F	6.6	5.8	2
Ruellia sp.	H	--	FL	.27		
Trichilia sp.	T	20	F	4.7		2
Tabebuia impetiginosa	T	162.5	P	2.6		
Talisia sculenta	T	29.1	F	.38		1
Thiloa glaucocarpa	T	112.5	P; T	1.6		
Zizyphus joazeiro	T	1.6	F	24.8	17.3	3
Indet.1	?	--	F	--	17.3	--
Indet.2	?	--	F	--	15.3	--
Indet.3	?	--	F	--	3.8	--

a- From the total of dung of Oitenta group collected from October 2000 to March 2002 (n= 52);

b- Based on the group scans.

*** Seed predation**

The most important change in diet during the dry season was the shift towards the consumption of more structural plant material (pith and tuber/roots). Accordingly, total consumption of plant matter increased significantly ($Z= -2.49$; $n=10$; $p=0.013$). Although the average time that the individuals spent feeding on tubers/root and pith was low (Fig. 32), the use of these resources might have been much higher had the group not received provisioned food. Interestingly, on some occasions when the group spent periods of time away from the feeding area (provisioned food) I perceived that the females from captivity were skinny or had lost condition in relation to the wild females. This may have resulted from their inexperience in tool use or lack of appropriate foraging skills (Chapter VI), which reduced their energetic intake and made tubers unavailable to them. Hence, it is reasonable to assume that the use of tuber and roots as food resources could be a key strategy for enduring the long dry season (see Chapter VI).

In the wet season, the age-sex classes had very similar diets (Fig. 35), but during the dry season there was somewhat more variation in the proportion of the different items consumed. Tubers/root were eaten only in the dry season. Adult females during the dry season consumed less fruit than did other age-sex classes, but differences among age-sex classes in the average rate of feeding on fruit were not significant (Kruskal Wallis ANOVA, $H= 1.1$ $df= 2$; $p=0.58$).

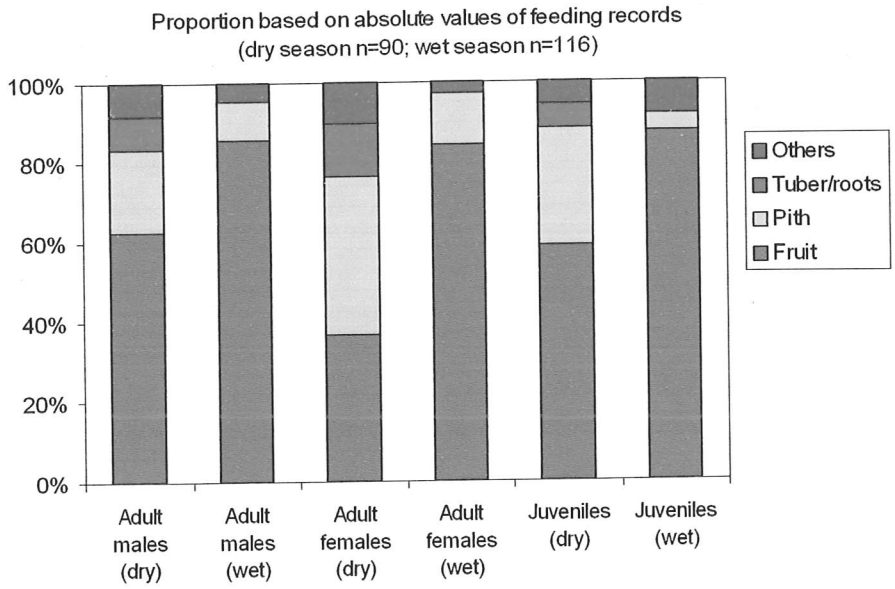

Figure 35. Percentage of scans feeding on different food items by the age-sex classes in each season.

Availability of food resources and use of space: The fruiting trees

Trees producing fruits, chiefly those producing fleshy fruits, are concentrated inside the canyons (Chapter III). I analysed the density and distribution of the trees producing fruits eaten by the monkeys and of the potential fruit food, i.e. trees producing fruits that were edible, but which I neither observed the monkeys eating nor found its seeds in the dung. I tallied the potential fruit trees species using the type of fruit and taste as indicative of their feeding potential for the monkeys, as well as reports of these being capuchin foods in the literature (e.g. Robinson, 1989; Freese and Oppenheimer, 1981). During the dry season, the density of trees producing fruit along the cliffs was similar to the canyons (Fig. 36), mainly due to the high density of *A. colubrina,* which accounted for 73.1% of the trees producing fruits. In the wet season, however, the number of trees/ha producing fruit in the canyons increased two

fold and was significantly higher in the Canyon habitats (χ^2= 8; df=1; p<0.01) by comparison to the Cliffs.

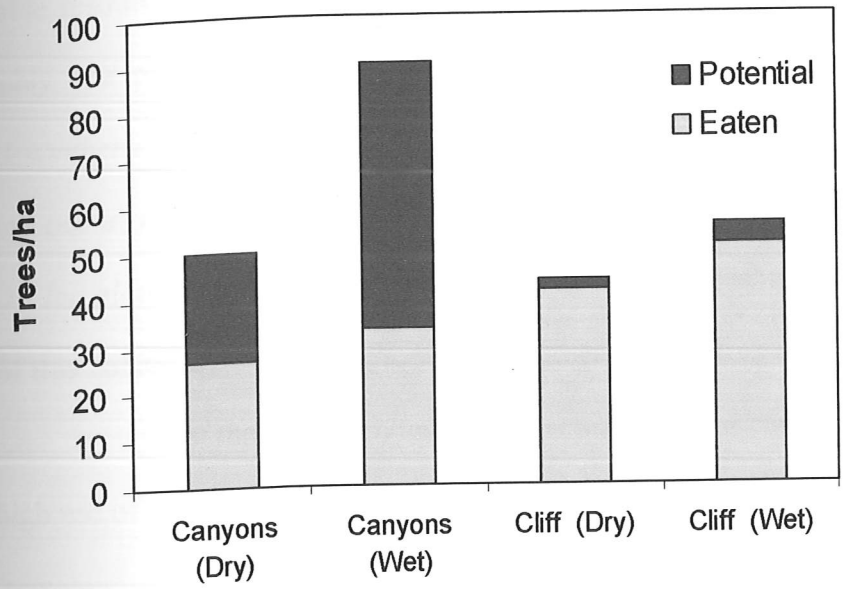

Figure 36. Density of trees (N/ha) producing fruit that were or could be eaten by the monkeys. I included only trees that produced fruit. Total area sampled 1.2 ha (only vegetation plots located in the monkeys' home range area and around it).

The monkeys consumed most of the fruits that were available from trees that grow along the cliffs, but I did not see the monkeys eating from potential food resources inside the canyons, nor did I find seeds of these canyons trees in their dung. Interestingly, in the dry season there were about 10 species of trees producing fruits in the canyons against just six tree species along the cliffs. As the canyons had a higher diversity and more trees producing fruits that were or could be eaten by the monkeys, I expected the monkeys to spend more time inside the canyons or at least to use them more frequently during the dry season. However, the monkeys spent over 96% of their time along the cliffs and just 1.6% of their time inside the canyons (n= 3,770 activity records, excluding feeding on provisioned food) and most of this was during the dry season. The availability of provisioned food could explain these results, but

fold and was significantly higher in the Canyon habitats (χ^2= 8; df=1; p<0.01) by comparison to the Cliffs.

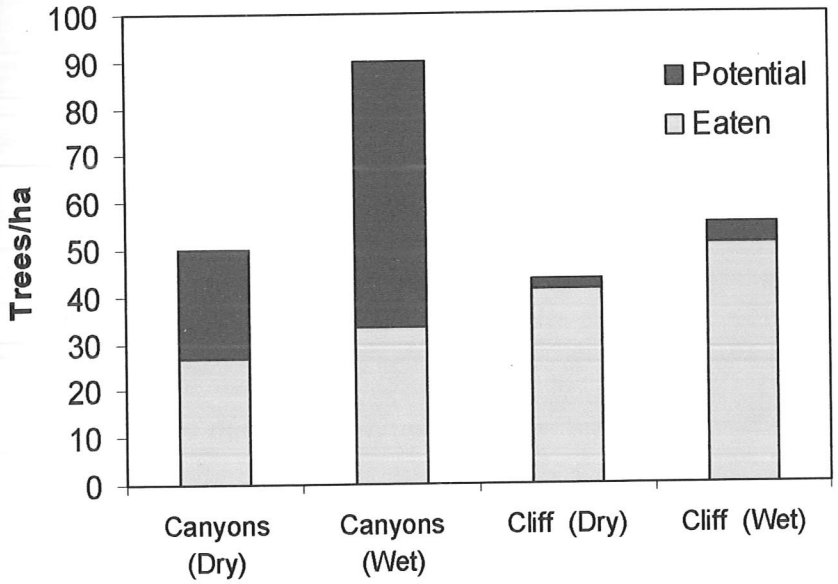

Figure 36. Density of trees (N/ha) producing fruit that were or could be eaten by the monkeys. I included only trees that produced fruit. Total area sampled 1.2 ha (only vegetation plots located in the monkeys' home range area and around it).

The monkeys consumed most of the fruits that were available from trees that grow along the cliffs, but I did not see the monkeys eating from potential food resources inside the canyons, nor did I find seeds of these canyons trees in their dung. Interestingly, in the dry season there were about 10 species of trees producing fruits in the canyons against just six tree species along the cliffs. As the canyons had a higher diversity and more trees producing fruits that were or could be eaten by the monkeys, I expected the monkeys to spend more time inside the canyons or at least to use them more frequently during the dry season. However, the monkeys spent over 96% of their time along the cliffs and just 1.6% of their time inside the canyons (n= 3,770 activity records, excluding feeding on provisioned food) and most of this was during the dry season. The availability of provisioned food could explain these results, but

the census data also indicate that other groups of capuchin monkeys were more frequently found along the cliffs (Chapter IV).

Copaifera cf *langsdorfii* trees, which fruit during the dry season and were a valuable resource for the monkeys, grow only along the cliffs. Their distribution is probably one reason why the monkeys spent most of their time there. Likewise *Anadenanthera colubrina*, another important fruit resource in the dry season (see above), occurs chiefly along the cliffs. Furthermore, the extremely high density of the tree *Thiloa glaucocarpa* along the cliffs could be another reason for the preponderant use of this habitat by the monkeys, since the tubers of this tree are an important food resource throughout the year. Yet, another more subtle factor could be contributing to the high use of Cliff habitat. In all of the Canyons, I observed a great number of nests of *Crematogaster* sp. ants, while the Cliffs were practically devoid of the conspicuous nest of this species. These ants are omnivorous, but they predate many invertebrates, and especially those that dwell inside dead wood and twigs on trees. It is possible that ants in the canyons reduced the availability of embedded insects for the capuchin monkeys. Thus, there is a possibility that the insects they prey upon are more abundant along the cliffs. Insect abundance is explored below.

Availability of food resources: Insect diversity and abundance

Insect foraging can be an important fallback resource during the dry season. Thus, I attempt to assess both diversity and abundance of this potentially critical food.

Nest traps

The solitary wasps and bees, which nest inside cavities, were more abundant along the Cliff and inside Canyons (Table 14). The size of these Hymenoptera ranged

from 0.5 cm to 1.5 cm. One of the largest Hymenoptera in the area is the carpenter bee (*Xylocopa* sp.), which probably has the largest larvae of all the species that nest inside cavities, but as it did not use the nest traps I could not determine its density. This species seemed to be common in all the different habitats of the park.

Almost twice as many individuals emerged from the tubes originating from the nest-traps set in the Canyon by comparison to the tubes that came from the traps along the cliff, but the difference only approached significance ($\chi^2 = 2.7$; df= 1; p= 0.099). Irrespective of species composition, there were remarkable differences between the Canyon and Cliff habitats. In the Canyon just one set of nest traps was used for nesting by the bees and wasps, and only during the rainy season, while along the cliffs, both sets of nest traps were used for nesting and 38.5% of the nests were made in the dry season.

Table 14. Identification and number of individuals of Hymenoptera that nested in the Nest-traps by area.

Species	Cliffs	Canyon	Plateau
Centris tarsata		5	
Sphecidae sp1	13		4
Sphecidae sp2	23		
Hymenoptera	3	50	

Pitfall traps

The number of invertebrates caught in the pitfall traps was similar across the different habitats sampled (Fig. 37). And there was no significant difference among the different habitats in the rate of invertebrates sampled, either in the dry season

(Kruskal Wallis ANOVA H= 0.78; df=2; p>0.5) or in the wet season (H= 2.8; df=2; p= 0.23). The Plateau had a lower diversity of invertebrates (Shannon index 1.33) than the Cliffs and Canyons (Shannon index 1.67 and 2.1 respectively). The diversity of invertebrates caught along the Cliff and in the Canyons was significantly higher than in the Plateau (t= -2.5 and t= -6; p<0.02). These results suggest a higher abundance of prey resources, i.e. an area that presents more species of insects or other invertebrates may have more 'food' items for the monkeys or other predators. In this sense, the canyons potentially presented more food resources than did the habitat along the cliffs, but the type of traps, their design (for dung beetles) and the small sample size suggest caution in making conclusions about insect prey abundance in the different habitats.

Nonetheless, the giant ant *Dinoponera quadriceps*, which is a predator of invertebrates and small vertebrates that dwell in leaf litter on the forest ground, was caught more frequently along the cliffs (42.3% of the invertebrates n= 213) than on the Plateau (32.4% n=71). These ants were very rare inside the Canyons; in five different Canyons I found their nests in just one, while along the cliffs and on the Plateau I frequently saw their conspicuous nests. These observations imply that food availability for this predator, at least on the forest floor, could be more abundant along the cliffs. This is still not a conclusive indication that the cliffs had a higher availability of food for the monkeys than did the other habitats. Analyses of abundance and diversity of birds that predate insects could provide further indications of which habitats are richer in terms of invertebrate food resources.

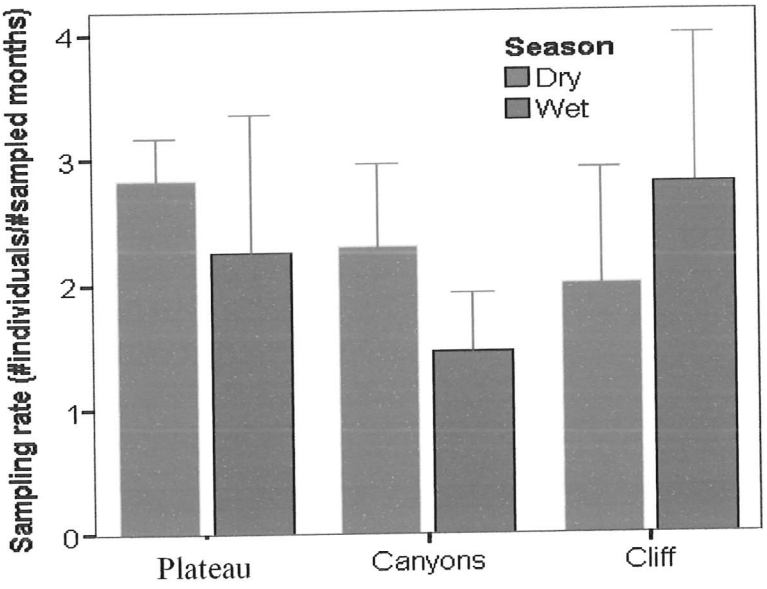

Figure 37. Sampling rate of invertebrates (see methods for details). Bars represent SE of the mean. There is no significant difference between any of the habitats (Wilcoxon test; all p> 0.5)

Indirect evaluation of insect abundance and diversity: The guild of insectivore birds

During the line transects, a total of 15 species of insectivorous birds were observed in the different habitats of the park (Table 15). These habitats were somewhat similar in the diversity of insectivorous birds, but the transects along the Cliffs and in the Canyons had a significantly higher diversity (Shannon index 2.06 and 1.95; t= -2.4 and t= 2.1; p< 0.04) than that found in the Plateau (Shannon index 1.54).

Table 15. Bird distribution and insectivore guild. P=Plateau; Cl= Along the Cliffs; Ca= Canyons. Body sizes are based on Sick (1993) and Ridgely and Tudor (1994)

Species	Body size (cm)	Guild	Habitat	Total individuals recorded
Celeus flavescens	27	Woodpecker	Cl	3
Colaptes melanocloros	26	Woodpecker	Cl; Ca	3
Dendrocolaptes platyrostris	25	Woodcreeper	Ca	7
Dryocopus lineatus	33	Woodpecker	Cl	3
Formicivora grisea	12	Antbird	Ca; Cl; P	22
Formicivora melanogaster	12.5	Antbird	Ca; Cl; P	5
Herpsilochmus pileatus	11	Antbird	Ca; P	21
Lepitocolaptes angustirostris	19.5	Woodcreeper	Ca; Cl	13
Myrmorchilus strigilatus	16	Antbird	P	5
Picumnus sp.	9-10	Woodpecker	Ca	2
Sakesphorus cristatus	14.5	Antbird	P	1
Sittasomus griseicapilus	14.5	Woodcreeper	Ca; Cl	3
Thamnophilus doliatus	16	Antbird	P	1
Thamnophilus punctatus	14.5	Antbird	Ca; Cl; P	23
Xiphocolaptes falcirostris	28	Woodcreeper	Ca; Cl	6

The insectivorous bird guild structure of the Canyons, Cliffs and Plateau was very diverse and probably reflected differential availability of insect resources (Fig. 38). Two aspects are significant here; a) the Plateau appeared to lack woodcreepers and woodpeckers or, more reasonably, their density was extremely low. For instance when I carried out the mammal censuses on the Plateau, I observed just five woodpeckers- *Colaptes* sp in over 180 km walked- b) along the Cliffs the proportion of woodpeckers is significantly higher (χ^2= 23.43; df=1; $p<0.001$) than in the Canyons.

The low stature, and consequent simplicity in forest layers of the vegetation in the Plateau (Chapter III), are most likely limiting the diversity of the insectivore bird guild through a reduction in niche and prey diversity. While the Cliffs, with a more diverse topography and vegetation, probably can supply sufficient resources to support the three insectivore guilds analysed here. The higher proportion of

woodpeckers along the Cliffs implies a higher availability of embedded resources. Moreover, the largest woodpeckers (*Celeus flavescens* and *Dryocopus lineatus*) were only observed along the cliffs, also indicating that embedded food resources were more abundant and diversified, and probably that larger embedded prey was more common.

Thus, the higher diversity of insectivorous birds and the presence of the largest woodpecker species just along the cliffs, coupled with a higher abundance of invertebrates and solitary Hymenoptera all indicate that this habitat is richer and this richness was a key factor in how *Cebus* allocates its time among habitats.

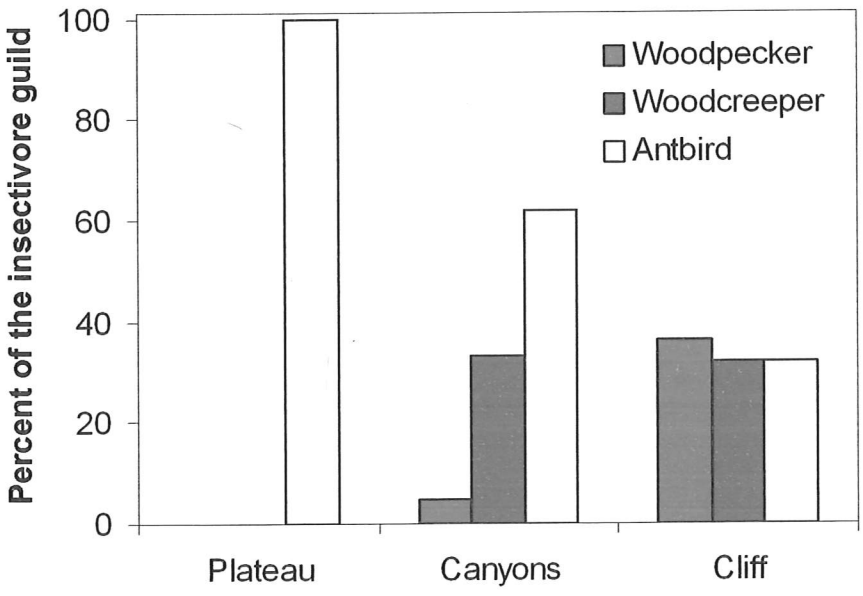

Figure 38. Variability of the insectivorous guild in the Park's three main habitats (n=120).

DISCUSSION

Individuals in the Oitenta group spend most of their time moving (37.1%), foraging (22.9% including tool use) and feeding (19.6%). These results are very similar to the activity budgets observed for other *Cebus* spp. (e.g. Robinson, 1986; Rose, 1994;Terborgh, 1983). The similarity between this partly provisioned group and other groups suggests that provisioning was not markedly skewing the behaviour of these capuchins. The monkeys dealt with food shortage during the dry season mainly through changes in diet, and the increased use of more tough or fibrous food in seasonally constrained diet has been observed in other *Cebus* species (Robinson, 1986; Chapman and Fedigan, 1990). Foraging strategies for obtaining protein rich resources during food bottleneck times appear to be important. Different species of *Cebus* increase their time spent foraging during the dry season, and insects became an important fallback in these times. Thus, when other resources became scarce and searching for insects becomes nutritionally essential increases in the time spent foraging would be expected. However, in this population, overall foraging activity was relatively constant over the months of the study (Fig. 39). This result could indicate a generally higher dependence on animal protein obtained through foraging activities, due to the low availability of other food resources, but it could also be an effect of the provisioning. As predicted, however, the most time and energy-demanding type of foraging – destructive foraging – was indeed more common during the dry season, and thus I suggest that provisioning probably was not greatly affecting the foraging pattern of the group.

What is interesting is that this provisioned group was able to maintain an activity profile that resembled that of "normal" capuchins, when they live in one of

the most extreme environments possible. It may be that the provisioning caused the activity profiles to converge with groups in richer areas, and that, in the absence of

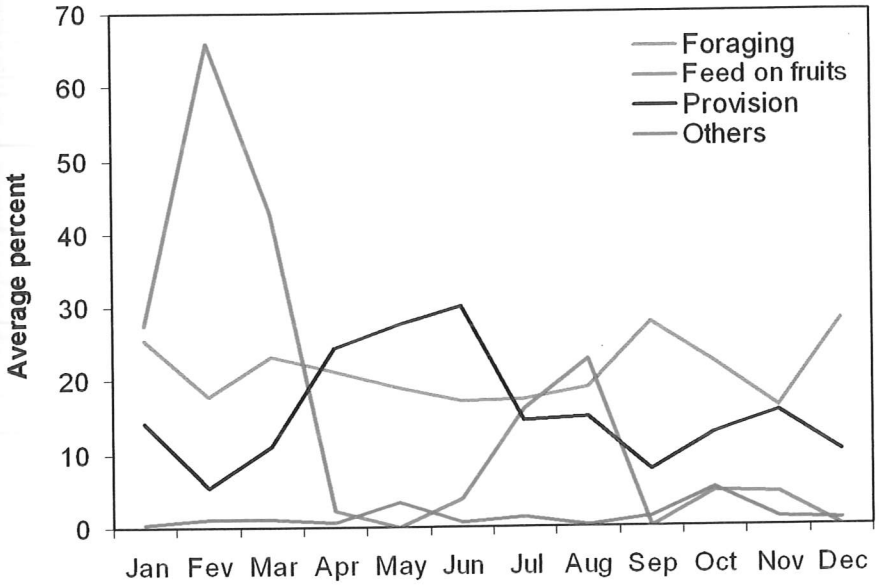

Figure 39. Monthly variability in foraging and feeding throughout the study. The variable others includes feeding on flowers, pith, tubers, vertebrates and larger insects. (n= 924 feeding observations).

provisioning, changes in activities to maximise energy intake and minimise expenditure might be expected. However, it is clear that the provisioning (while valuable and indeed contested, as shown by the invasion of the provisioned group) was unnecessary for the existence of capuchins in this area. Six other groups contributed data to the food species and habitat preferences, and the provisioned group did not appear to behave in any way atypically relative to these unprovisioned groups.

During the dry season (May-Oct.), the time spent in destructive foraging increased and adult males spent more time in this type of foraging. A major factor leading to this sex difference could be the size and energetic value of the prey items.

Adult males in *C. capucinus* also spent significantly more time in destructive foraging (Rose, 1994), which could result from the possibility of obtaining a higher energetic return from their activities.

The exploitation of embedded resources (primarily social insects, solitary wasps and bees, larvae of Cerambicidae, Passalidae, Scarabeidae and other groups of beetles that dwell inside dead branches or trunks) may increase the probability of survival for the monkeys in this particularly dry habitat. Wood-boring insects have a very high calorific value, they are relatively larger prey items (ranging from 4 cm to 9 cm) and they can be found in clumped distributions (Dufour, 1987). Thus, although the time and opportunity costs of obtaining these prey items are likely to be high, they are a rich, reliable food resource and the morphological and behavioural adaptations of *Cebus* enable them to harvest those taxa efficiently.

It follows that, if wood-boring insects are a reliable resource and destructive foraging is a fitness increasing activity, then destructive foraging should be more frequent in populations living in dry areas. Contrary to this prediction, however, *Cebus* species living in wet areas (Amazonia forest) exhibit higher proportions of destructive foraging (Table 16), regardless of species differences (see Terborgh, 1983). This maybe due to a higher density of wood-boring insects in these habitats. Unfortunately, detailed interspecific comparisons of foraging are hampered by problems of definitions; for instance Fragaszy (1986) includes grabbing, biting, chasing, and other patterns as active foraging (destructive), while Rose (1994) considers breaking branch and stripping bark as heavy foraging (destructive) and included the opening of stems in manual forage. Despite these confusions, the proportion of 'less active' (manipulative) and 'more active' (destructive) foraging reported by Fragaszy were similar to results obtained by Robinson (1986). For *C.*

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capucinus I could not find any report of the proportion of time that they spent in each type of foraging, although Rose (1994) cites that males spend 3.7% of their foraging time in heavy foraging and females devoted only 0.5% of foraging time for destructive foraging. Lamentably, she did not provide a break down of proportion of time spent in each foraging category. These values are extremely low when compared with the group I studied, where males spent up to 22.2% of their foraging time in destructive foraging and the females up to 13.3%.

Table 16. Proportion of different types of foraging in some wild population of *Cebus*.

Species	Habitat types	Foraging types			Source
		Destructive	Manipulative	Visual	
C. apella libidinosus	Dry forest	16	31.5	48.5	This study
C. apella	Wet forest	44.3	31.8	23.9	Terborgh (1983)
C. albifrons	Wet forest	32.4	43.7	24	Terborgh (1983)
C. olivaceus	Dry forest	25.8	58.9	25.8	Robinson (1986)*
C. olivaceus	Dry forest	28	57	15	Fragaszy (1986)

* Based on appendix II.

Insects are usually considered as a non-clumped resource for primates, but the embedded ones probably have a more clumped distribution as sites for nesting may be clumped. These results have important implications for understanding *Cebus* evolution and ecology. From an evolutionary point of view, the exploitation of embedded resources by *Cebus* could have had major impacts on their social system and cognitive abilities. This is especially true for *Cebus apella*, which has morphological adaptations, such as strong jaw musculature and thick tooth enamel, associated with the exploitation of nuts and tougher food (Janson and Boinski, 1992). In this species, females show a preference for the dominant male. This preference is determined by the ability of the alpha male to limit others' access to food resources during times of scarcity and his tolerance of a particular female or likely juvenile

offspring feeding nearby (Janson, 1984). Janson (1985) highlights the importance of within-group food competition and the ability of the alpha male to monopolise food (mainly palms products) as a driving factor shaping social organisation of *C. apella*. The control of resources by the alpha male allows him to offer benefits that subordinates cannot either obtain or control. Yet, the foods secured (fruit, flower or pith of palm trees) apparently do not have low-density clumped distribution. Palms are one of the species with highest density in Amazonian forest and in wet forest sites in Panama (Condit *et al.*, 2002; Peres, 1994b), many species occur in high-density clumps (Fragoso, 1997). Thus, it could be hard for a single male to securely monopolise all of these food for himself, the females and juveniles. Although most *Cebus* spp. species currently occur in wet forests, their morphological adaptations, their unique destructive foraging behaviour and the use of large aseasonal embedded resources suggests that these adaptations may have arisen for life in drier or more seasonal environments, where the selective pressure for efficiently using such resources would be strong. Terborgh (1983) and Janson (1984) implied that *C. apella*, the most robust species, has specialised for the exploitation of palm, mainly palm nuts, but palm trees have restricted distributions (see Peres, 1994b). For instance, they essentially do not occur in my study site, while dead branches, tree bark, and the accompanying cohorts of wood-boring insects and other invertebrates occur in almost all type of habitats. These embedded resources can play a crucial role sustaining energy balance in drier habitats. Thus, it can be suggested that *Cebus* evolved in the context of the selective pressures operating in drier habitats.

Use of the forest strata and foraging for embedded resources

Cebus generally use the middle storey of the forest. Although I suggested above that it could be a strategy to avoid predation by larger raptorial birds, for instance the eagle, *Harpya harpya* which is the main predator of *Cebus* in Amazonian forest (Janson, 1986), another reason for this preference could be related to foraging for embedded resources. Stratification in the distribution of these embedded resources may exist between the different levels in the forest. Growing trees leave dead branches behind as they gain height, the branches in the shades are doomed to die, and then these can become places for nesting bees and wasps, and for beetle species that require dead wood as food for their larvae (e. g. Passalidae). Thus, the microhabitat influencing insect distribution may account for the spatial distribution of the monkeys.

Sex differences: The consequences of sexual dimorphism or reduction of feeding competition?

In different species of *Cebus*, the adult males spend significantly more time on the ground than do females (*C. capucinus*: Fedigan, 1993; Rose, 1994; *C. olivaceus*: Fragaszy, 1986, 1990; Robinson, 1986;). Fragaszy (1990) suggests three possibilities for the preponderant use of the ground by males: a) due to their larger size, males are less vulnerable to predators ; b) males have a high foraging return from using the ground; c) males use the ground more because they are heavier than females. Fragaszy provides support for the possibility of increased predation risk on the ground and shows that males are more willing to face these risks, but males also have a greater foraging return on the ground; over 30% of larger invertebrates caught by *C.*

capucinus were on the ground (Rose, 1994). Interestingly, sex differences in use of forest strata apparently do not occur in wet forest. Terborgh (1983) discusses in detail many differences between the sexes in foraging and use of substrate, but he does not mention differences in use of space. Apparently these differences are more marked in dry areas, but there is a dearth of detailed studies for drawing any comparative conclusions.

I suggest that sex differences in foraging could be a mechanism to reduce feeding competition. Thus, in drier areas, the differences between the sexes in use of the ground should be more marked, but I did not find any significant age-sex class difference in use of the ground. Yet, there are two confounding factors that could be affecting use of the ground. One is the provisioning that might reduce the need for sex-specific niche separation by reducing food competition. The second factor is more subtle. Adult males showed a strong trend to spend more time in digging foraging than did females (Mann-Whitney test $U=7.5$; $p= 0.066$, two-tailed, pooled data $n_1=4$, $n_2=10$) and this type of activity leads to finding valuable tubers and root resources. During digging activity, the females and juveniles tended to stay significantly closer to the adult males possibly in order to scrounge food remains from the patch found by the male. This could operate to reduce any sex differences in use of the forest strata, but my sample size is very small. Uncertainty is inherent in these data and no amount of statistical sophistication will remove it. However, good sense and parsimonious explanations can give accurate indications into how these monkeys efficiently exploit a harsh habitat for survival and, at the same time, reduce the conflicting interests between the sexes in how to obtain the most valuable types of food without incurring high costs via competition.

Cognitive abilities and survival in a harsh environment

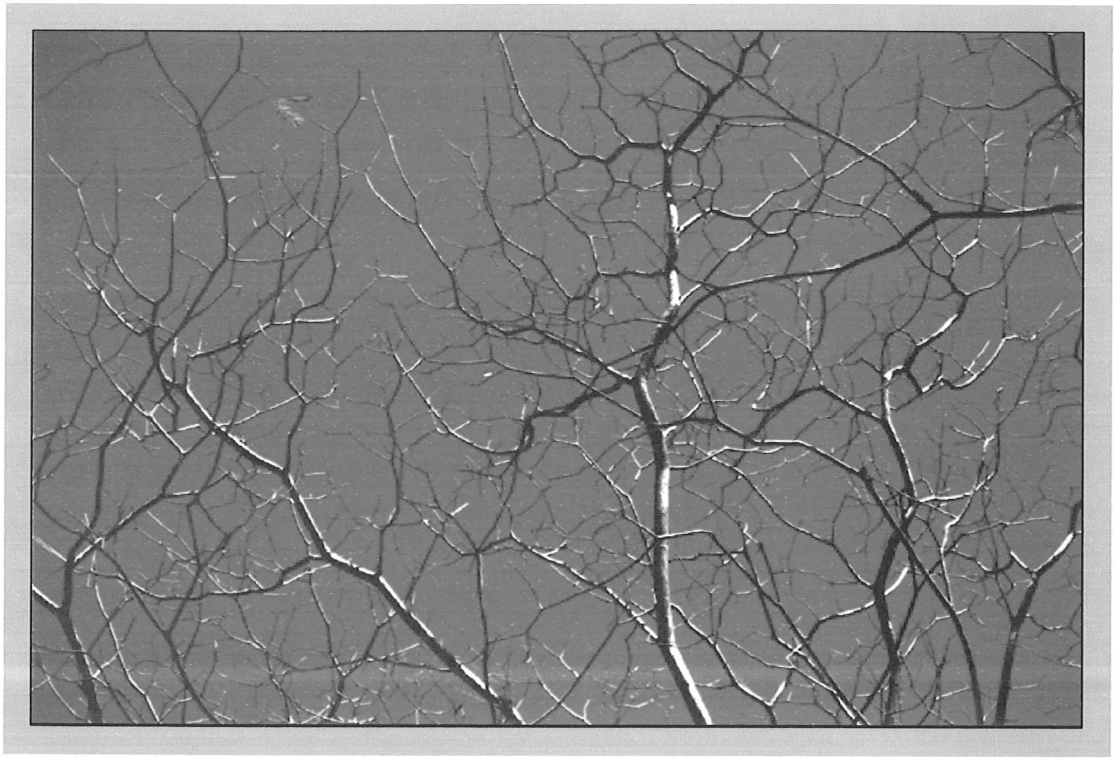
Parker and Gibson (1977) suggested that the extractive foraging accelerated and enhanced brain enlargement in primates, although there have been a number of criticisms of this hypothesis (see Chapter VI). The brain of *Cebus* is amongst the largest relative to body mass of any non-human primate (Janson and Boinski, 1992).

Certainly, it can be suggested that the cognitive abilities of *Cebus apella libidinosus* are key features allowing them to survive in the Caatinga forest. In the harsh, unpredictable environment of the Caatinga, developing novel strategies to cope with constantly changing conditions could be very important for survival (e.g. Lee 2003). One innovation to enhance energy balance is the extensive tool use seen in this population. For instance, the use of a stone to open a nut could reduce the time taken to open it, which ultimately would mean more food was eaten in less time, leading to an improvement in the returns from foraging activities. In chimpanzees, tool use greatly facilitates feeding efficiency during times of food scarcity (Yamakoshi, 1998). During times of food scarcity, the capability to use tools is also advantageous in order to procure edible foods, which are not otherwise accessible. For instance, tool use enabled a community of wild chimpanzees at Bossou, Guinea, to consume two out of three keystone species during times of fruit scarcity (Yamakoshi, 1998). In the Caatinga area, the use of tools allowed the monkeys to obtain different types of resources and this probably was a key component of their foraging strategy (see Chapter VI).

SUMMARY

- The activity budget of the study group was similar to activity budgets observed in other capuchin species, suggesting that provisioning was not influencing rates of behaviour.

- The monkeys spent over 22% of their time on the ground, a higher value than reported for other capuchin populations, and during the dry season use of the ground increases.
- Foraging as a means of obtaining resources accounted for 22.3% of total activity time. Foraging for embedded resources, such as insects inside dry branches or tubers, increased during the dry season when other resources are not available. Sex differences were marked in foraging behaviour, with males concentrating foraging effort on manipulative and destructive foraging. Apparently males obtained a higher return from these activities and when engaged in more difficult foraging tasks (destructive and digging) other individuals in the group were found closer, possibly to obtain food remains.
- The group exploited 26 plant species for fruits and other parts. Considering also opportunistic observations and dung analyses from other groups, the number of plants used as food resources was low when compared to capuchin population living in other dry forests type. Interestingly, the monkeys spent most of their time along the Cliff habitat, which has a lower diversity of trees and lower density of trees producing fruits when compared to the Canyons habitat. The preponderant use of the Cliff habitat was due to a higher availability of invertebrates resources, evidenced by the different taxa of insects caught in nest-traps and pitfalls. Indirect evidence, through evaluation of the abundance and diversity of insectivorous birds, corroborates the high invertebrate richness in the Cliff habitat, particularly of wood-boring insects. Moreover, along the Cliffs there is an extremely high density of tubers (from *Thiloa glaucocarpa*), which are an important food resource.
- The exploitation of insects embedded in dry branches may increase the probability of survival for the monkeys in the Caatinga dry forest. These prey items tend to be large and have a high calorific value. Cognitive abilities, however, are the key component allowing capuchin monkeys to survive in the Caatinga dry forest, since the use of technology allows access to a greater variety of food resources.



The bare branches of Tabebuia impetiginosa *during the dry season*

Chapter VI

TOOL TECHNOLOGY AND SURVIVAL IN A HARSH HABITAT

INTRODUCTION

Capuchin monkeys are the only monkey species to match great apes in the extent of their tool use (McGrew and Marchant, 1997; Tomasello and Call, 1997). Nonetheless, their cognitive capacities to solve tool use problems have been ardently questioned in a series of studies by Visalberghi and colleagues (e.g. Visalberghi and Trinca, 1989; Visalberghi and Limongeli, 1994,1996). In these studies, they provided capuchin monkey groups with a series of tool-related problems, such as inserting stick in a transparent tube to obtain a food reward, but the monkeys made numerous mistakes. On many occasions the monkeys selected unsuitable objects to be used as tool and the errors persisted across blocks of trials. These results and further experiments comparing capuchin monkeys with chimpanzees and children (Visalberghi *et al.,* 1995), both of which choose the right tool to solve a specific problem, led to the belief that capuchin monkeys lack an understanding of the causal relation in using the correct tool to solve a problem. In contrast to chimpanzees and humans, capuchin monkeys do not extract knowledge from previous experience and use this to solve new problems (Visalberghi and Limongelli, 1996; Visalberghi, 1997). When capuchin monkeys solve a tool-related problem it is rather a consequence of their dexterity and manipulative propensities than an understanding of cause and effect; they solve problems by trial and error (Visalberghi and Limongeli, 1994, 1996).

Nevertheless, there are a series of counter-examples indicating that capuchin monkeys, or at least *C. apella*, do have an understanding of cause and effect. For instance, Westegaard and Suomi (1993) reported how a captive group of capuchin monkeys (*C. apella*) cracked nuts with a stone and used sticks to extract the nut "meat", using a tool set similar to wild chimpanzees. After the nuts were cracked, the capuchin monkeys increased the selection of sticks and also altered their selection based on the demands of the task implying an understanding of cause and effect. Similarly, Anderson (1996) shows how captive capuchins (*C. apella*) can select and modify sticks accordingly to the problem to be solved and he provides strong support for the suggestion that capuchin monkeys do have a mental representation for tool use, i.e. an understanding of cause and effect. More recently, Lavellee (1999) tested a group of capuchin monkeys (*C. apella*) on their ability to solve a probing task in a naturalistic captive settling and found that the monkeys modified the branches and also chose the tools to be used in an apparently non-random fashion. In all of these examples, the monkeys consistently chose and used appropriate tools for solving a task, implying an understanding of the task requirements.

Boinski *et al.* (2002) raise another possible reason for inefficiencies in solving tool-related problems in captive capuchin monkeys; the manipulative activity itself can reduce the stress from captivity and mistakes in completing the task can prolong the duration of the manipulative activity, which is a reward in itself. There is another important point that has not been addressed adequately in the literature: rearing conditions can have a profound effect on cognitive development. Capuchin monkeys reared in more naturalistic settings seem to use tools in correct ways, without making

mistakes (e.g. Jalles-Filho *et al.* 2001). Chevalier-Skolnikoff (1989) pointed out that wild-born capuchin monkeys were quicker and more likely to solve tool-related problems. In chimpanzees it has also been noted that wild-born subjects perform better and learn faster than do captive-born subjects (Brent *et al.*, 1995). Environmental conditions (social, physical and nutritional) which affect brain growth and neurological development may influence abilities in cognitive tasks (e.g. Rapoport, 1999).

Despite this alternative perspective, the studies of Visalberghi and colleagues led van Schaik *et al.* (1999) to claim that the lack of tool use in wild monkeys stemmed from the lack of causal understanding and inefficient observational learning techniques; they have a "lesser" intelligence in relation to great apes, which exhibit customary use of feeding tools in the wild. Recently, Garber and Brown (2004) presented to a wild group of *C. capucinus*, a tool apparatus that required probing to access the food reward and the monkeys failed to solve the problem. They explained the failure of the monkeys in using tools as a consequence of lacking of causal understanding. In the model of van Schaik *et al.* (1999), the general precondition for use of feeding tools is extractive foraging, which is reflected in manual dexterity and this explains the frequently observed tool use by diverse species of monkeys in captivity. In their model they include social tolerance and understanding of cause and effect as key components for the use and making of feeding tools, and these two key elements explain the tool use observed in wild populations of great apes. However, I suggest that the model of van Schaik *et al.* (1999) is not based on firm grounds, since the main differences between tool use in monkeys and apes have not been conclusively demonstrated and remain debatable (e.g. Tomasello and Call, 1997).

The lack of tool use in wild groups of monkeys, and particularly capuchin monkeys, still demands an explanation and remains a cognitive enigma as Tomasello and Call (1997) state: "One of the greatest mysteries in the study of primate cognition is why so many species are skilful tool users in captivity, yet do not use tools extensively in wild".

As noted above some authors consider frequent tool use in captive animals as mechanism to escape boredom (Bekoff, 1989; Panger, 1989) and as a consequence of high availability of time for experimental manipulative abilities (Beck, 1980). However, there are several hypothesis based on ecological and environmental factors that try to explain the lack of habitual tool use in wild groups of monkeys, particularly in capuchin monkeys. These hypotheses are generally easily refutable. For instance, one frequent explanation is that an arboreal life style precludes the use of tools (e.g. hammer and anvil stone for cracking seeds); capuchin monkeys spend much time in trees, there are no free hands to hold a tool and they lack a stable substrate for tool activity. It is also suggested that they have few opportunities to have access to both tools and tool sites in order to discover tool use by trial and error (McGrew and Marchant, 1997; Visalberghi, 1987; Visalberghi and McGrew, 1997). Panger (1998) used this suggestion as an explanation for the lack of tool use in wild *C. capucinus*. Thus, a high degree of terrestriality coupled with co-presence of nuts and stones could be an essential ingredient for the appearance of tool use in wild populations (Ottoni and Mannu, 2001; Visalberghi, 1987). Nonetheless, Defler (1979) observing *C. albifrons* in Colombian semi-deciduous forest did not find a single event of tool use in over 500 contact hours. In this area there were plenty of stones, palm nuts were common and consumed by the monkeys, and the monkeys would

sometimes spend up to 50% of their time on the ground. Similarly, Rimoli *et al.* (2002) reported on a group of *C. apella* that collected the husked fruit of Lecythidaceae in trees up to 30m in height and then pounded these on the tree trunk or against stones on the forest floor. These monkeys spent up to 49% of their foraging time on the ground, but they never used tools in the sense of using a detached object to reach an aim (see Chapter V for the definition of tools used throughout this thesis).

Ecological constraints (Beck, 1980) represent another commonly-invoked hypothesis to explain a lack of tool use in wild monkeys. For instance, Boinski *et al.* (2000) pointed out that the needs for anti-predator vigilance and the time allocated to foraging by wild capuchin monkeys could reduce the potential time investment in object manipulation. It thus follows that monkeys living in more luxurious forests, with a high or almost constant availability of food resources should engage in some form of tool use, yet capuchin monkey population living in these types of habitat failed to exhibit tool use (e.g. Terborgh, 1983).

During times of food scarcity or in more impoverished habitats, however, the capability to use tools could be advantageous in order to procure edible food not otherwise accessible. Yamakoshi (1998) observed that in a community of wild chimpanzees at Bossou, Guinea, the ability to use tools was particularly important for obtaining essential food resources during lean times, and tool use was much more frequently observed during periods of year when major fruit foods were lacking. In the woodpecker finch (*Cactospiza pallida*), tool use (twigs or cactus spines used to pry arthropods out of tree holes) apparently was restricted to populations living in the arid zone of Santa Cruz Island, Galapagos archipelago, where there was low food abundance compared to the humid areas (Tebbich *et al.* 2002). The use of tools in this population contributed significantly to their

subsistence, particularly during the dry season when tool use increased and the finches obtained 50% of their prey with help of tools. Interestingly, Langguth and Alonso (1997) in one anecdotal report of tool use in *C. apella libidinosus*, suggested that tool use could be an important foraging strategy during food bottleneck periods.

The key point is that studies on capuchin monkey groups living in a harsh environment, where the use of feeding tools could have direct implications for survival, are lacking. Use of tools is energetically costly and risky in terms of time activity and it would be predicted only to occur if the benefits are higher than the costs (e.g. Tebbich *et al.* 2002).

Aims:

To assess the tool technology of a population of capuchin monkeys in a dry habitat;

To evaluate seasonal patterns of tool use and possible link with resource availability;

To evaluate possible sex differences in tool use and possible relation with energy requirements.

METHODS

Details of the area where the monkeys live and the group's history were given in Chapter V. A description of vegetation and biodiversity in these areas was provided in Chapters II, III and V.

In this chapter I analyse feeding tools only, i.e. a detached object used with the aim of obtaining food or to facilitate an activity related to obtaining food. I saw many events of tool use as an aggressive display (hitting a rock surface with a stone, releasing the stone in my direction while performing aggressive calls) that were quite common during the habituation process of the monkeys, however, I do not consider these events here.

During an event of tool use, I recorded the identity of the performer, the locality, and relevant information about the tool type, food or context of tool use. I also videotaped tool use and analysed it in details for duration and sequence, but the total footage was relatively short with about 3 minutes of tool use. For carrying out the analyses, I collated the data from the scan and focal samplings, as well as all events of tool use derived from all the observation time spent with the monkeys (total of 397.5 hours, from October 2000 to March 2002) and which were not included in the focal and scan samples. Due to the conspicuousness of this behaviour, both by sight and sound (when the monkeys used stones) it was likely that I missed relatively few events while following the monkeys.

Most of the data on tool use are presented as individual hourly rates, which I calculated based on the total time spent with the group. For instance, in March 2001 I obtained a total of 35.4 contact hours with the group and I used this value to calculate individual rate of tool use/hour for this month. In using this method, I assumed that all the

individuals in the group were always in sight when being observed, and in the case of tool use, which was a very conspicuous behaviour, this is probably a reasonable assumption.

RESULTS

Using feeding tools

I observed tool use in three groups widely distributed throughout the area; in the case of one group it was more than 18 km apart from the other two groups. Tool use seemed to be widespread throughout the area. I found indirect evidence of tool use by a fourth group, namely a stone hammer and scattered open seeds of *Manihot* sp. around a wooden anvil (Fig. 40). The monkeys in this area used three types of feeding tools: (a) **probing** - branches or twigs used to probe tree holes and rock crevices - I observed this in two groups in the area; (b) **cracking** – use of stones to crack open diverse materials (seeds, dry branches etc), this was observed in all three groups; (c) **digging** - the use of a stone for digging up tubers/roots – this was the most commonly seen tool use. I saw digging with a stone in three wild groups and in Baixa Grande, I frequently found characteristic holes around *Thiloa* trees, where the monkeys dig for tubers. I observed a total of 154 detailed feeding tool use events, and 94.8% were from Oitenta group. I observed Oitenta group from October 2000 to March 2002 for a total of 392.4 hours. Since I observed the Oitenta group more frequently and systematically, I based the following analyses on data collected during one year (January to December 2001) totalling 312.3 contact hours.

Figure 40. Seeds of *Manihot* sp. open with a stone hammer. This photo was taken in Esperanca Canyon, about 15km from the Oitenta Group area

Tools for survival

During one year, I recorded a total of 134 tool use events in the Oitenta group, 0.43 events^{-h}, which gives 5.1 tool use events each day. Another four instances of potential tool use were heard (a stone being hit against the soil) and these surely were related to tool digging (see below), but here I analysed only the visually-observed instances of tool use.

The Oitenta group used branches for probing into tree holes and rock crevices and in 42.8% of occasions (n= 21) the branch (twig) was modified by removing leaves or stems before being inserted into the holes in trees or rock crevices. The most versatile of the tool technology of these monkeys was cracking, when the monkeys used a stone to crack open seeds (38%, n= 26), dry branches (15.4%), or dry cassava (*Manihot esculenta*) tubers (42.3%), which were provided by the park authorities, into small pieces to facilitate eating. On many occasions the monkeys obtained a piece of the dry cassava, carried it to a rock or put it on a wood surface, got a stone and cracked it in small pieces before eating. The monkeys also used stones to try to crack dry *Thiloa* tubers (3.8%). In

one astonishing event, the alpha male (Boludo) used a stone to destroy a rock matrix (a crevice) and 15 minutes later, when I could observe him again, he was eating a lizard (*Tropidurus semiteniatus*) that uses rock crevices for protection. The resourcefulness of these monkeys was even more evident when Boludo, during the dry season, obtained a cactus (*Pilosocereus piauhyensis*). Then, carrying it by the root to a rock outcrop, he smashed the middle of the cactus with a stone and apparently consumed part of the soft pith inside. The juveniles that were nearby ate part of the cactus after Boludo moved away. The most frequent type of tool use, and for me also the most remarkable, was digging with a stone (Fig. 41). The use of a stone as an aid for digging up tubers or roots is a kind of tool use not described yet for any population of primates either in captivity or in wild, except for humans. Usually, monkeys dig the surface with their hands, but on occasions they got a stone as digging tool. On these occasions, an individual typically held the stone with one hand and hit the ground quickly for 3-6 times (about 3 to 7 sec.), while simultaneously scooping away the soil with the other hand, then released the stone and dug for up to a maximum of five minutes using both hands. Sometimes, after releasing the stone and digging for a while, the monkey would get the stone again and hit the ground quickly to help digging. Another common pattern was to hit the ground quickly with a stone held in one hand or both, then release the stone and dig using both hands. These activities seemed to loosen the soil and facilitate the digging activity. A digging bout was considered to be a period of continuous soil scraping at a given site, regardless of the number of times a stone was picked up, used and released whilst at the same site.

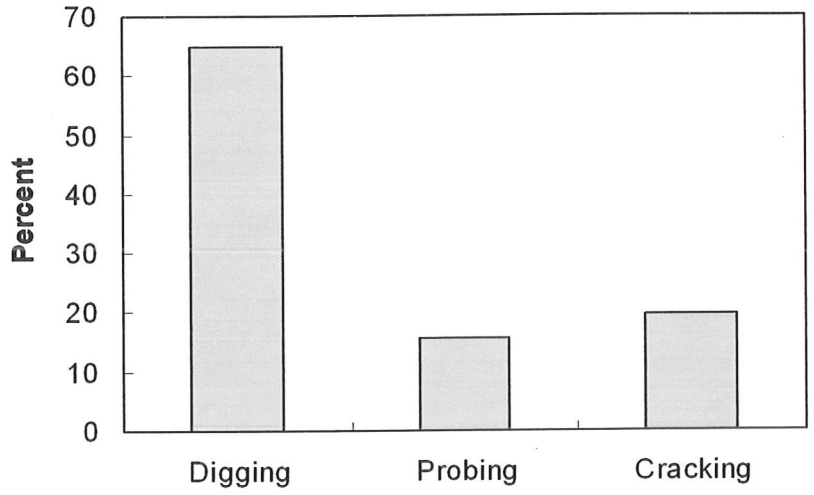


Figure 41. Proportion of the different feeding tools employed by the monkeys (n=134).

Tool use and seasonality

Notwithstanding the long dry season and associated food shortage (see Chapters III and V) there were no significant differences in tool use between the wet and dry season (Mann-Whitney test, U= 14, N=6 months; p= 0.52), suggesting that tool use could be a key component to survival in this harsh habitat throughout the year.

From month to month, however, there was great variability in the rate of tool use by the monkeys (Fig. 42). The Park Administration provisioned my main study group (Chapter V) and this was an important confounding factor potentially masking seasonal changes in tool use. Despite this provisioning, the use of feeding tools by the monkeys was linked to the availability of food in the forest. Throughout the year there were decreases and increases in availability of different resources; the rates of tool use apparently mirrored this rhythm. For instance, in March, which shows a marked drop in tool use, the monkeys increased their consumption of *Zizyphus joazeiro* fruit. In June-

August the monkeys ate the leguminous pod of *Anadenanthera colubrina,* and seeds of *Copaifera* cf. *langsdorfii* (an important resource during the dry season) were frequently found in their dung (Chapter V). During this time, rates of tool use were generally lower. In November, well after the onset of rainfall, there was an explosion in caterpillar numbers - a resource heavily exploited by the monkeys. This coincided with the major decline in rates of tool use. The high frequency of tool use in February, a month with many trees species fruiting, was associated with a marked decrease in the provisioning. This population of capuchin monkeys used tools customarily, but the only type of tool used consistently in every single month was digging.

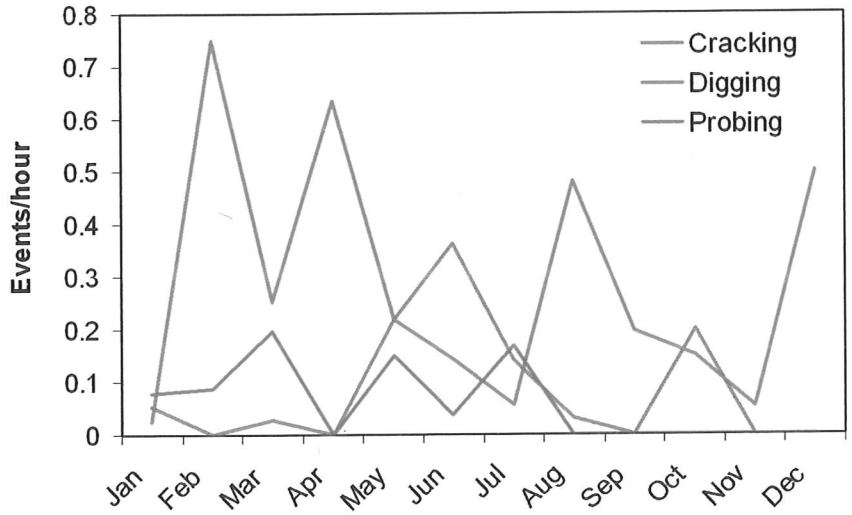


Figure 42. Monthly variation in the rate of tool use. The values were calculated as the total events of tool use observed divided by the total hours in contact with the group each month.

Age-sex classes differences

Adults males (n=2) were responsible for the majority of tool use (Fig. 43) and performed over 63% (n= 134) of all tool use observed. Indeed, they presented significantly higher rates of tool use than did the other age-sex classes both in the dry

(Kruskal Wallis ANOVA, H= 13.31; df= 2; p= 0.001) and wet seasons (H= 24.13; df= 2; p<0.001). Interestingly, probing was performed almost exclusively by adult males; the only female to exhibit this behaviour was Peta (a captive female released in the area), who once used a twig as a probe, but the behaviour was very brief (about 15 seconds) and she used both hands, in contrast with the adult males. Apparently she was copying the behaviour of one of the males. Generally, the females had very low rates of tool use.

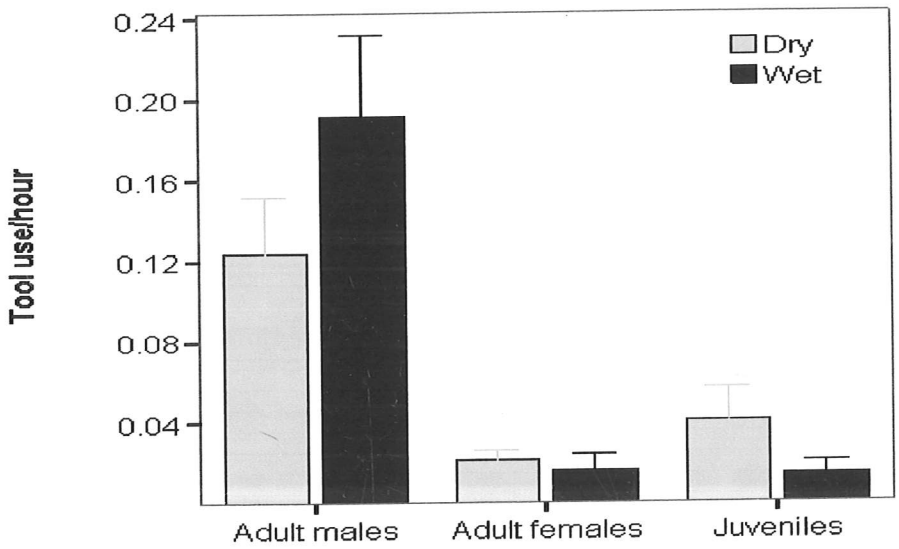


Figure 43. Individual average tool use rate by age-sex class in each season. Bars show standard error.

Time spent in tool use and rewards from the activity

In 60.4% of tool use events, I was able to record the total time that the animals spent in the activity. When using a tool, the monkeys could spend up to five min (range 3 sec to 5 min). Tool bouts for which duration was recorded (n= 81) last an average of 55.5 sec (±SE 6.8). Digging usually lasted an average of 59.5 sec (±SE 8.3). The duration of

digging is very conservative, since on some occasions when I located an individual it was already engaged in a bout of digging. Probing in trunk holes or crevices in rock surface lasted an average of 60.9 seconds (±SE 18.4), while tool cracking usually was briefer lasting an average of 25 seconds (±SE 8.4). Overall, duration of tool use tends to be longer during the rain season ($\bar{x}$= 64.5 sec ±SE 9.3; n= 48) than in the dry season ($\bar{x}$=42.4 sec ±SE 9.6; n= 33), but this difference was not significant (t= 1.6; df= 79; p=0.11).

In 62.1% of the tool use events (n= 134) I was able to record the reward, i.e. extracting a tuber/root or eating something, and the type of reward (tuber, insects or other food item), but in over 27% of the events I was unable to determine if the monkeys obtained any reward from their tool use activity. The difficulty in recording whether there was recompense from effort was due to poor visibility, or aggressive and other behaviour by the monkeys that distracted the observer or the monkeys.

In those tool use activities (probing, cracking and digging) where I could determine the outcome, scored as yes or no (n= 82), the proportion of obtaining a reward was surprisingly low (36.6%). Considering just digging (n=49), however, the success of the monkeys was slighter higher; they terminated their activity by obtaining a tuber/root in 40.8% of the cases.

Of the different types of tool used, probing presented the highest proportion in failing to obtaining a reward (Fig. 44), but the higher proportion of non-recorded rewards for both digging and probing events could mask the true proportions of reward derived from tool use.

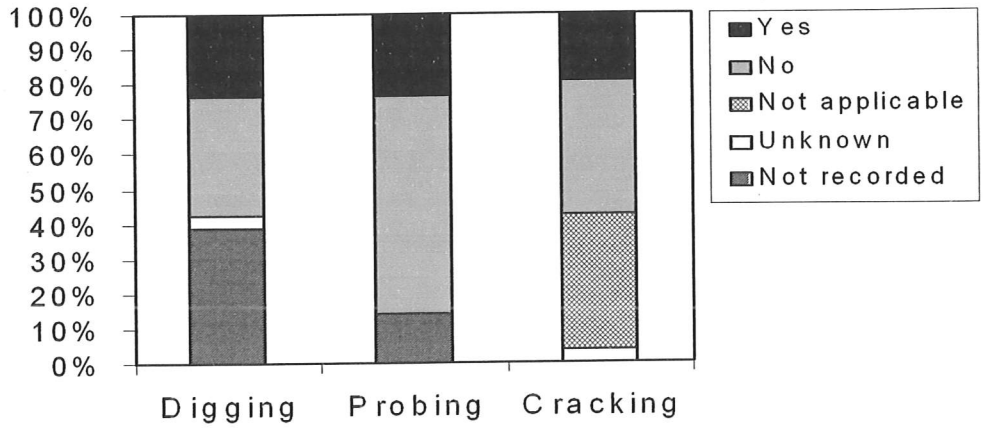


Figure 44. Rewards from the different kinds of tool used for obtain food. The category 'not applicable' refers to cracking provisioned cassava tubers (which was always YES) and 'unknown' when I was unable to determine if an individual obtained or not food through tool use.

Seasonal differences in time spent digging

Digging was the only tool behaviour used by the majority of the animals and was observed throughout the study, thus allowing for more fine grained comparisons between time spent in the activity and rewards. I recorded the duration of 55 digs (dry season n= 18; wet season n= 37). During the wet season, digging activity lasted an average of 67.1 sec (±SE 11.7) and in the dry season 43.7 sec (±SE 7.17). There was a slight trend to spend more time digging in the wet season ($t=1.7$; $df= 52.4$; $p= 0.09$). In the wet season, males and females did not differ in the amount of time digging and in the dry season females tended to spend more time in digging than males, but the difference was not significant (Fig. 45).

For a total of 42 digs I recorded both duration and reward (dry season n= 12; wet season n= 30). When the consequence of the activity was a reward (a tuber or root), the

monkeys tended to spend more time digging ($\bar{x}$ = 77.1 ±SE 18.7, n=16) than if they did not gain a reward ($\bar{x}$ = 51.6 seconds ±SE 11.1, n= 26), but the difference is not significant (t= -1.246; df= 40; p= 0.22). However, during the dry season the monkeys invested significant more time in the digging when they obtained a reward (t= -2.59; df=10; p=0.027).

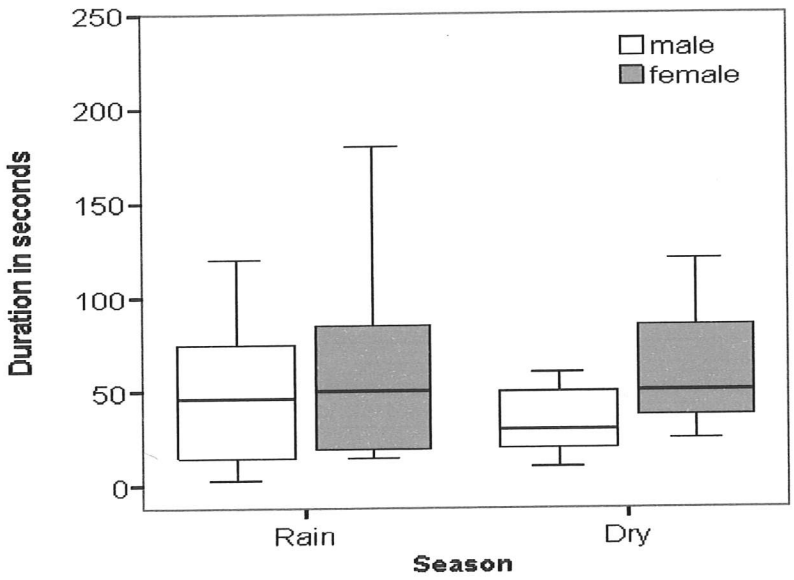


Figure 45. Median duration of time spent digging in wet and dry season. Boxes shows upper and lower quartile and lines represent the lowest and highest observed values.

Obtaining food through tool use

The main observed reward from tool use was the extraction of underground tubers and roots (Table 17). Tubers of the tree *Thiloa glaucocarpa* accounted for 65% of the tubers eaten, and this tuber seemed to be highly sought after. This tree is very common in

the area (Chapter III) and probably is the staple resource during food bottleneck periods (Chapter V). It was not possible to carry out analyses of the nutritional value for *Thiloa* tubers, but data from the literature indicate that these tubers have a high caloric value and thus the payoff for the investment of effort in terms of time and energy in their extraction is very high (O'Connel *et al.*, 1999). The *Thiloa* tree's tubers look like an onion, with layers of a white matter (probably carbohydrate) intercalated with fibrous walls (Fig. 46). These tubers weight an average of 13.9 g (±SE 4.6; n= 10) with a average length of 3.25 cm (±SE 0.42) and width 2.3 cm (±SE 0.37), but I have seen larger tubers about the size of an apple.

The holes made by the monkeys digging usually were shallow, with a depth ranging from 3 to 8 cm ($\bar{x}$= 4.7cm; n=5) and an average length of 11-24 cm. There were a number of old holes scattered in the area which were 12-15cm deep.

Table 17. Percent of rewards obtained through the three main tool behaviours (n=30).

Type of reward	**Type of tool use**		
	Cracking	Digging	Probing
Cactus (*Pilosocereus piauhyensis*)	3.3		
Drinking (water?)			10.0
Insects (?)	3.3*		1.3
Lizard	3.3		
Seeds (sp. unknown)	6.7		
Tuber/Roots		66.6	
Unknown			1.3

* Extracted from dead branches cracked open with help of a stone.

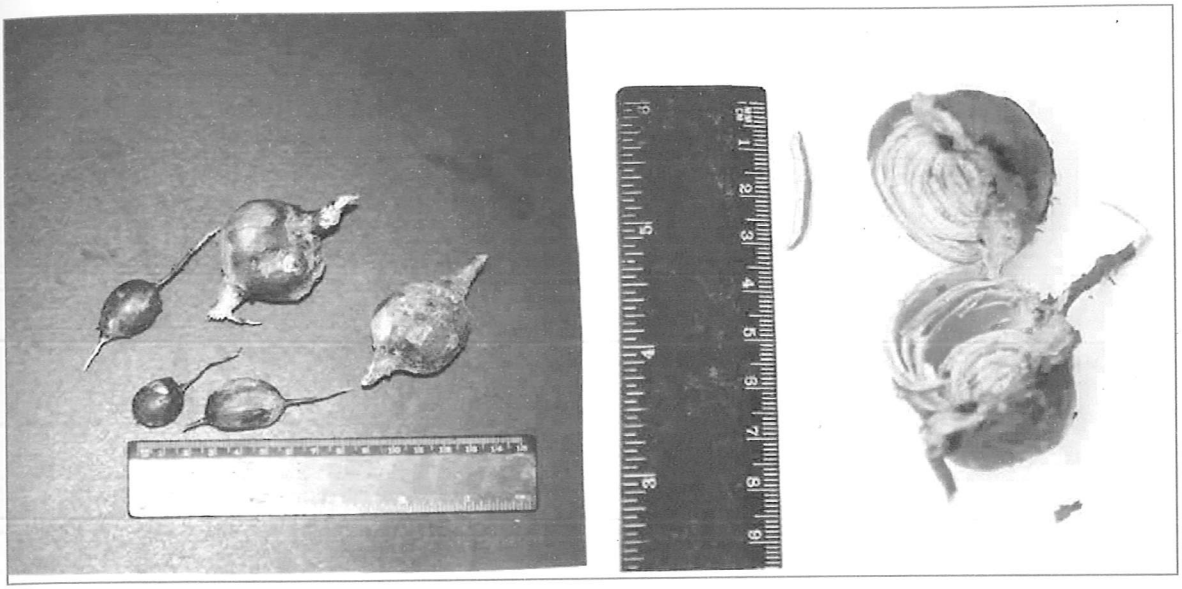


Figure 46. Tubers of *Thiloa glaucocarpa*. The most frequently found were small sized.

Performance of captive animals and the learning of tool use

The three captive females had extremely low tool use by comparison with the two wild females. One of the captive females released in the area (Desc) never used tools and the others used a tool in 17.2% of the total tool use events recorded for the five adult females (n=29). The captive females were not observed getting a reward from tool activity and they seemed to be learning how to use the tools. The only captive female to use a stone for digging was Clarinha. Yet, she performed the behaviour very briefly and differently from the wild individuals. The first time I saw her in what looked like a tool use was on 20th April 2001. In this occasion she approached the wild male Adt, who was digging with a stone. He left the digging place and Clarinha went to the hole he had made, smelt the hole, took a branch (or root), smelled it and hit the ground twice with it. About one minute later, she approached again the male Adt, who was digging in another place, and remained in proximity observing him. When this male left the place, Clarinha

again went to smell the hole and the stone the male had used for digging. She turned the stone and afterwards hit the ground 3-5 times and then went away. In another event, Clarinha used a stone to hit 3 times the ground, but every time the stone hit the ground she dropped it.

The female Peta sometimes observed carefully the tool activities of the alpha male. For instance, on 10th October 2001 while the male Boludo was digging, Peta was observing him very close (about 10cm) and after 20 seconds she moved to another place. In the same month, Boludo was cracking a dry trunk with a stone and Peta observed his activities very closely (<10cm); when Boludo left the trunk she smelled it and then moved away. Although this female did not exhibit tool activities, except as described above, it is possible that her curiosity towards tool activities performed by other individuals would led her to experiment with some kind of tool use similar to that of the wild monkeys in the area.

On many occasions, when the alpha male (Boludo) was engaged in tool digging the youngest capuchins, and occasionally adult females, carefully observed his activities and sometimes ate the remains of tubers/root found by the male. The released captive juvenile engaged in tool use behaviour similar to his wild peers, but he seemed to be still learning the tool use techniques and never obtained a reward from his activity.

When adult males dug or were eating tubers/roots, the juveniles were in close proximity and ate the food remains. In Oitenta group, when adults were engaged in tool use if other individuals were close typically these would be the juveniles (see Fig. 28 in Chapter V). Unfortunately, as the scan sampling occurred at long intervals (see Chapter V) it resulted in a low number of tool use events (n=30) with proximity records.

Considering only instances in which adults were engaged in tool activities, another individual was nearby (0-2m) in 54.2% of the cases (n=24). This small sample size precludes more detailed analyses of the spatial patterns associated with tool use activities. Nevertheless, when I collated the data with distances regarded as very close (< 1m) and close (1-2m), based on focal, scans and all occurrence events, in 62.8% (n=35) of tool use events there was another individual very close, paying attention to the activity. The juveniles were the main observers (68.2%, n=22) of tool activity in close proximity (< 1m) while females were very close in 31.8% of these tool use episodes. In Baixa Grande area, I also observed this pattern of proximity during tool use; juveniles and females stayed closed to individuals engaged in tool use and sometimes ate food remains originating from these tool activities.

This type of inquisitive behaviour performed mainly by immatures is also frequently observed in baboons (Altmann, 1998; King, 1991; Hill, 1962). Ottoni and Mannu (2002) observed in a semi-free ranging group of *Cebus apella* that during tool use, the immatures (infants and juveniles) were the main observers of the tool use activities performed by others in 76.3% of the episodes. I think it is reasonable to assume that a similar pattern was going on in my study group.

Although I obtained a low frequency of tool use and proximity patterns from the scan sampling, it is worth comparing these with foraging activities. There is a trend for juveniles and females to stay nearer adult males (0-2m) engaged in tool use, while during foraging activity they tend to keep more apart (Table 18).

Table 18. Proximity to adults that were engaged in tool use or foraging. The tool use and foraging values originated from the scan sampling. For foraging I used a cut-off distance class of 8-15meters. M= males; F= females and Juv= Juveniles. Notation example: M-F= males were performing an activity and the nearest neighbour was a female.

Distance classes	Tool using (%)				Foraging (%)			
	M-F	M-Juv	F-M	F-Juv	M-F	M-Juv	F-M	F-Juv
>0-2m	63.6	100	0	66.6	36.1	39.4	15.5	30.3
3-7m	27.3	0	100	33.3	40.9	42.4	40.1	44.3
8-15m	9.1	0	0	0	22.9	18.2	44.4	22.9
Total frequency	**11**	**3**	**1**	**3**	**61**	**33**	**187**	**122**

The tool technology of capuchin monkeys: understanding of cause and effect?

The tool technology of this particular population of capuchin monkeys is astounding. On many occasions I was amazed, while observing tool use episodes, by their proficiency and intelligent use of feeding tools to solve a series of feeding problems as in some of the examples I provided above. All of the wild monkeys demonstrated an understanding of the causal relation of using a tool and solving a specific problem related with acquisition of food. In this sense, some episodes are noteworthy. For instance, in November 2000 Lampiao (the previous alpha male, see Chapter V) got a stone and smashed a piece of sugar cane, and afterwards swallowed the juice. On another occasion (29/01/01), the male Adt took a piece of dry branch (about 18-20 cm), put it on a rock outcrop, got a stone and hit the branch three times in a gentle way. Then he ate something from inside the branch (probably the brood of some species of ant such as *Camponotus* spp., *Solenopsis* spp. or *Zacryptocerus* spp., which usually nest inside dead branches). On

15th of July 2001, the male Boludo took a stone, located 1.5m away from the dry branch to be opened, hit the branch twice and then opened the branch using his teeth. The use of a stone to crack or facilitate the opening of dry branches or even trunks, seemed to be an important technique in the destructive foraging repertoire of this group.

There were, however, two more revealing examples of the causal understanding of tool use. First, the manufacture of probing tools in which a monkey got a branch and then removed leaves and lateral twigs before using it as a probing stick. A nice example of this occurred during the dry season (09/07/01); the alpha male Boludo found something inside a trunk hole then gave a call attracting the wild females and juveniles (they were circa 6-8 m from him). After five minutes striping the hole in the trunk and trying to break it, he moved one meter away, got a dry branch, removed the twigs and used it as a probing tool. He manipulated this stick in the trunk hole for about five minutes and then moved away, followed by the females and juveniles[1]. I believe that the successful modification of branches can be viewed as a strong evidence for a mental representation of the tool needed. Indeed, as van Schaik *et al.* (1999) pointed out the modification of an object to reach a goal requires hierarchical planning and mental representation.

The second example, and perhaps more enlightening, was the choice of stones for digging. Most of the time the monkeys seemed to pick any stone for digging, but on a few occasions they moved away looking for a stone, even when there were stones around the hole being dug. This implies a mental image of an object that will be used to solve the problem, or perhaps improve their performance, and also the choice of the correct tool to

[1] Possibly he located inside the hole a small rodent or a peculiar frog from Caatinga (*Corythomantis greeningi*) that use tree holes to endure the dry season (Navas *et al.*, 2002).

be used. For example, on 3rd Aug 2001, the male Boludo was digging with a stone, then after four minutes he stopped and went looking for another stone. He returned with a bigger stone to the same place and dug using this stone. On another occasion (15/12/01), this male was digging with bare hands, then stopped looked around, walked over 1.5 m to a previous hole, got the stone he had used there and returned to dig with this stone. This particular stone had a more pointed shape and probably sped up and facilitated the digging activity. I do believe these monkeys provide the strongest evidence so far that capuchin monkeys, or at least *Cebus apella*, have an understanding of the causal relation of tools and the outcome of their use.

DISCUSSION

This particular population of *Cebus apella*, used tools almost on a daily basis to solve a series of food-related problems, and this is the only wild monkey population to exhibit a customary use of feeding tools. The use of a stone to help digging was particularly surprising. Among apes there are reports of gorilla digging up shoots of bamboo during the dry season (Casimir, 1975) and chimpanzees, from the Tongo forest in Congo, during the dry season dug up moist tubers (Lanjow, 2003), but even these apes have yet to be observed to use tools for digging up tuber/roots. Interestingly, the average individual rate of probing (0.007^{-h}) in my study group was similar to that reported for orang-utans (0.0089^{-h}) by van Schaik *et al.* (2003) and the tool-use rate (events/hour) is significantly higher than anecdotal reports of tool use recorded during long-term studies in some capuchin monkey population (Table 19).

Table 19. Tool use rate (events per hour) in wild groups of capuchin monkeys.

Specie	Habitat type	Tool type	Rate	Source
C. albifrons trinitatis	Evergreen (Rainforest?)	Leave as a cup	< 0.001	Phillips (1998)
C. apella	Rainforest	Branch 'hammer'	0.001	Boinski *et al.* (2001)
C. apella libidinosus	Dry forest	Probing	0.067	This study
C. apella libidinosus	Dry forest	Digging	0.28	"
C. apella libidinosus	Dry forest	Cracking	0.083	"
C. capucinus	Dry forest	Probing	0.003	Chevalier-Skolnikoff (1990)

Tools for all seasons: the importance of technology for survival

I was expecting a higher rate of tool use during the dry season, when resource availability is drastically reduced (see Chapter III and V), but instead tool use was almost constant throughout the year and did not differ significantly between seasons. Perhaps this constancy in tool use is an indicator of its importance for survival. A more plausible explanation for this aseasonality could be linked to food provisioning, which reduces the need to resort to technology for obtaining food. Although tool use is an important component of the foraging strategy in this capuchin monkey population, it comprised only 3.2% of the foraging time (n=946 foraging records, including tool use events) and possibly this was an effect of provisioning. Had this group not been provisioned, the rate of tool use could have been much higher and would perhaps present a more seasonal trend, but I did not find any relation between monthly rate of tool use and average proportion of time feeding on provisioned food (Spearman r_s=0.15; n=12). Possibly a series of factors were affecting the use of tools, including provisioned food and the availability of resources in the forest. If there are plenty of resources around, then the use of tools can be reduced since using tools can be costly in terms of time and energy (e.g. Tebbich *et al.*, 2002). The use of stones seems to be energetically demanding; the average (±SD) weight of a stone was 165.1g ± 183.1 (n=14) and even using tools, the failure in obtaining food was relatively high (see Fig. 44). And yet the use of tools can greatly improve the diet (e.g. Yamakoshi, 1998) and even though energetically demanding, the net benefit of tool use is much higher in terms of energy gain (Gunther and Boesch, 1993; Tebbich *et al.*, 2002). Thus, the constancy in tool use in this population of capuchin monkeys implies that the habitat in which they are living is impoverished in terms of food

resources (see Chapter III and V) and that a strong selective pressure for using tools must be at work.

In this area the monkeys used about 41 plant species as foods (Chapter V) and the use of tools probably increased the consumption of at least three species, namely *Thiloa glaucocarpa* (tuber), *Manihot* sp. (seeds) and *Hymenaea courbaril*[2] (fruits). In the case of *Manihot*, its seeds are extremely hard and probably could be opened only through the use of tools. The use of probing sticks allows for extracting insects, honey, or vertebrates from inside tree holes and rock crevices and similarly the use of stones to crack different kind of material while looking for food probably guaranteed access to a number of resources or at least improved the foraging efficiency. Thus, the use of technology allowed access to resources otherwise unavailable. Moreover, I think that by hitting the ground with a stone the monkeys could obtain some kind of auditory cue about the location of tubers. During periods of drought in the Caatinga, the human inhabitants look for the tubers of *Spondias tuberosa*, which store water, by hitting the ground with a walking stick and according to the sound, the tuber can be easily located and dug up.

In the Caatinga harsh conditions, ecological pressure is the mainly factor driving the cognitive capabilities of *Cebus*. The use of a stone to crack open hard seeds/fruit or to help dig up tubers could reduce the time spent obtaining foods, which ultimately means more food eaten in less time, leading to an improvement in the returns from foraging activities.

[2] This tree did not fruit during the study period, but I found indirect evidence (accumulation of broken fruits and stones around) suggesting the use of tools.

Intra-group sex differences in tool use: energetic costs and the vagaries of learning

The adult males used tools significantly more frequently than did females. Moreover, only adult males used probing (except for one incident with a released captive female). These results are in striking contrast with findings in chimpanzees, in which females use tools significantly more than do males (Boesch and Boesch, 1984; McGrew, 1992). McGrew (1992) suggested that this sex difference probably was a consequence of differential energetic requirements; females have major reproductive energy costs and by using tools they have access to nutritious and reliable food resources, i.e. nuts and social insects. On the other hand, Boesch and Boesch (1984) hypothesised that the chimpanzee sex differences in tool use stemmed from the greater strength of the males, which could reduce their fine motor control over the tools, and from differences in sociability; males favour social contacts with their companions and keep stopping their activities to monitor other males nearby and if these leave the site, they will follow. These authors, however, did not discard the energetic hypothesis.

My results for capuchin monkeys are puzzling. The females in the group were either pregnant or with dependent infants (Chapter V), hence had higher energetic requirements than did the males. The main reward from tool use was the extraction of underground tubers, chiefly *Thiloa glaucocarpa*. It was not possible to carry out analyses of the nutritional value for *Thiloa* tubers, but as noted above the tubers have a high nutritional value (especially carbohydrates) and the payoff for the effort of time and energy in their extraction is considerable; thus for females they could be a key resource (O'Connell *et al.*, 1999). And yet tool use to extract tubers and overall was

preponderantly a male activity. Male predominance in tool use behaviour in *C. apella* has also been observed in naturalistic captive settings (Jalles-Filho, 1995; Jalles-Filho *et al.*, 2001), but other studies, in a more restricted captive condition, did not find any sex-differences (Westergaard *et al.*, 1998). The predominance of male tool use in captivity has been explained in term of social inhibition of others by the dominant male who could monopolise the tool apparatus (Jalles-Filho, 1995). However, in the group I followed, the females and juveniles usually were at closer proximity with the males when males were using tools and most of the time they ate food remains. I never saw males monopolising the site where they used tools. Another possibility could be linked to predation risk; most of tool use episodes occurred on the ground and females can be more vulnerable when on the ground (Fragaszy, 1990). Boinski *et al.* (2000) used this reasoning to explain the predominance of males in pounding husked fruit in a population of *C. apella* in Suriname. They did not find any sex differences in skill or coordination for opening the hard-shelled fruits and reasoned that this extremely noisy activity could attract a number of predators and since females are more averse to predation risk, they would avoid or greatly reduce this activity.

The predation risk hypothesis probably is not the best explanation for the extreme sex difference I observed in tool use, since in my study group females spent as much time on the ground as males (Chapter V) and were typically close to the males during tool use. Moreover, predation avoidance cannot explain the sex differences observed in captivity. A more plausible explanation should take into account both the costs/benefits in terms of time and energy, and incorporate the peculiar mating system of *C. apella*. Thus, I suggest two possible explanations for this discrepancy:

1- Females could be scavenging from the effort of the males (Parasite females), eating food remains and saving energy. The males are relatively bigger and stronger than females and can obtain resources unavailable to females and immatures. For instance, Robinson (1986) observed that sometimes individuals of *C. olivaceus* uprooted *Cochlospermum vitifolium* saplings of up to 2 meters height in order to eat the root. This action was performed mainly by the larger males in the group; smaller individuals attempt this procedure, but rarely succeed. In this context, the marked sex difference can make sense in terms of the social system of *Cebus apella*; the alpha male monopolises food resources and allows only some females and his offspring to feed on that resource (Janson, 1984).

2- Tool use probably is very demanding in terms of energy, and the cost could outweigh the benefits; the low rate of success in obtaining food through tool use can be more serious for the females, so tool use would be a last resort for food bottleneck periods. The reward from tool activity (Fig. 44) provides support for this hypothesis. For instance, probing had the lowest return in obtaining a food item, and it was almost exclusively employed by males. Moreover, the weight of stones used by females was significantly lighter than those used by males ($t= 2.28$; $n=14$; $p= 0.04$).

These sex differences in tool use can then be understood through these intertwined possibilities, but a more speculative possibility is that these differences could be just a product of chance and same-sex copying behaviour. For instance, in all capuchin monkeys species usually males leave the group and females are philopatric (Fedigan,

1993; Jack and Fedigan, 2004). In leaving their groups, males might carry with them the particular idiosyncrasies of their group (e.g. probing with sticks) and young males in the new group would copy the behaviour. The higher rate of tool use in males could then be explained by high attention that youngsters direct to same-sex adult; a sex biased learning mechanism (see Lonsdorf *et al.* 2004).

The copying behaviour possibility could explain why, in some captive populations of capuchin monkeys, males are more manipulative and use tools more frequently than females, while in others there is no sex difference (e.g. Jalles-Filho, 1995; Visalberghi, 1988). If among the founders of a captive group only the females used tools or were more manipulative, then their offspring would tend to behave likewise, particularly the daughters. Conversely, if both male and females founders are equal in manipulative and tool activities, then their offspring will present similar trends for these behaviours. Fragaszy and Visalberghi (1989) conducted some experiments with captive groups of *C. apella* to assess the effect of social learning, i.e. if observation of a skilled tool user would enhance the performance of other individuals in the task, but they did not find any evidence that a social model could led to learning how to use tools. However, my speculative suggestion is that sex differences in tool use or manipulative behaviour in capuchin monkeys could originate from a 'hardwiring' to play more attention to activities of same sex individuals and copy their behaviour. A critical window during ontogeny could exist during at which tool use or other particular manipulative activities must be learned. Wastergaard *et al.* (1998) suggest that for using tools (probing) capuchin monkeys must be exposed to an appropriate tool site during an important, but probably not critical, learning period. This hypothesis is testable in captive conditions, for instance

monitoring the development of offspring from capuchin couples in which both males and females are equally manipulative and tool users compared with couples where only the males use tools or couples where only females are tool users. Recently Lonsdorf *et al.* (2004) described a four-year longitudinal study of termite fishing (probing) and how it is learned in a wild community of chimpanzees in Gombe, Tanzania. They observed that the sex differences in fishing stemmed from the fact that the daughters play more attention to the activities of their mother than do the young males, who prefer to play around the termite nest instead of observing the probing techniques. Interestingly, Brent *et al.* (1995) studied two groups of captive chimpanzees, comparing their ability to use tools, and did not find any sex differences in tool use. As a final point, Reader and Laland (2001) found that adult male primates generally were more innovative than were females, and thus could have a trend for using more tools.

Understanding cause and effect: why do other wild capuchin populations not use tools?

One of the main points of this chapter is that ecological factors, namely low food abundance and the unpredictability of finding food in dry areas, were the trigger mechanisms favouring tool use as a means to enhance foraging and for meeting the energetic requirements of these monkeys. However, other populations of capuchin monkeys have been studied in dry forests and tool use is absent in these populations. For instance, in the dry forests of Costa Rica in over 17000 contact hours with *C. capucinus* (data from table 1 in Panger *et al.*, 2002) there is just a single record of tool use (probing), while for groups of *C. olivaceus* living in the dry Llanos a single event of tool use has yet

be recorded, despite extensive studies in the area (e.g. Fragaszy 1986; Miller, 1996; Robinson, 1986; de Ruiter, 1986). In the latter case the lack of tool use is noteworthy, since the monkeys frequently dig up snails from a depth of about 10cm, an activity performed mainly by males (Fragaszy, 1986). What has led some populations of capuchin monkeys to use tools extensively, while in others tool use is practically absent? I believe that this discrepancy is explained by a differential availability of food resources amongst these forests.

Although seasonal changes in food supply occurs to a greater or lesser extent in all primate environments, variation tends to be more marked in dry habitats (e.g. Oates, 1987; van Schaik et al., 1993; Chapter III). Thus, in dry forests food shortage could have a more drastic effect on the life of a primate than in a rainforest environment. Using diversity as a proxy for overall food availability, the Caatinga dry forest presents a markedly low diversity when compared with other Neotropical dry forests (Chapter III). Moreover, the average annual rainfall in the Llanos is about twice (1450 mm) that of the Caatinga dry forest, and higher rainfall can be translated into higher food productivity (Murpho and Lugo, 1986; Chapter II). *Cebus olivaceus* in the Llanos also use many more species of plants as food resources than does the group I studied (Chapter V), again suggesting a restricted availability of food resources in Caatinga. Similarly, in the dry forest of Costa Rica the annual rainfall is around 1500 mm and tree diversity is much higher than in the Caatinga (Chapter III). Interestingly, *Ateles geoffroyi* a highly frugivorous species occurs in the dry forest of Costa Rica, implying that there is sufficient fruit availability for a large-bodied primate even in the dry season. Thus, the risk of starvation could be considered as the mother of all inventions. The strong reliance on tool

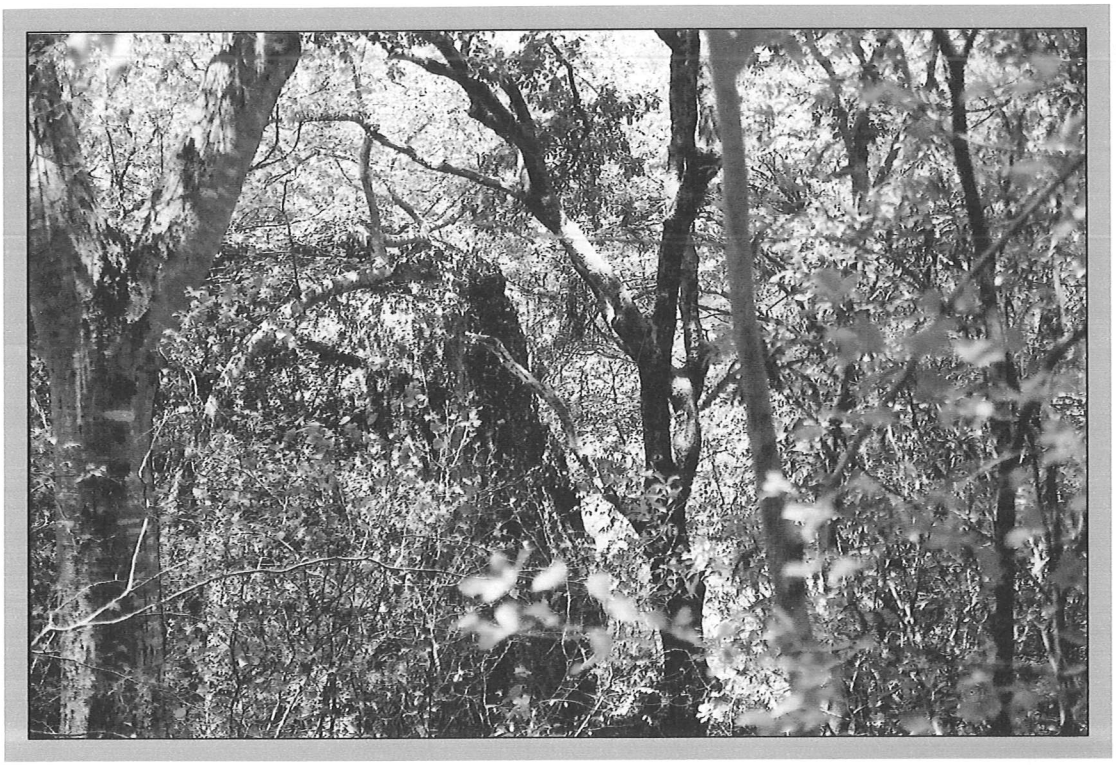
use to acquire food resources is the key strategy allowing this population of capuchin monkeys to survive in the Caatinga dry forest

Nevertheless, there is a small detail, albeit of capital importance for the logical thread of this thesis; digging up tubers or roots is a frequent foraging activity of baboons and these underground plant organs are staple food, especially during the dry season (Altmann, 1998; Norton *et al.*, 1987). Macaques can also make extensive use of underground resources (Iguchi and Izawa, 1990), but despite ten of thousands of hours of field observation baboons and macaques have not yet been observed using tools for digging. I have suggested and implied throughout this thesis that the essence of tool use is inextricably linked to extractive foraging and life in a harsh habitat. Yet baboons and macaques are also extractive foragers and baboons in particular live in areas much drier than Caatinga. The almost complete absence of use of feeding tools by these species is paradoxical. Understanding the reasons behind this discrepancy could provide important insights into the evolution of tool use in the hominins and also of how differential selective pressures could affect the expression of tool use. I will discuss this problem in the next and final chapter.

SUMMARY

- Technology was the most important aspect of the daily life of capuchin monkeys for their survival in the harsh conditions of the Caatinga dry forest. The monkeys in this area used three types of tools: (1) twigs and branches for probing into rock crevices and holes in tree trunks; (2) stones for cracking or to pulverise different materials; and (3) stones for digging up tuber and roots.

- Tool use events in the focal group occurred at a rate of about 5 events/day. This is the only monkey species to present customary tool use in wild. Despite the long dry season and associated food shortages, tool use did not differ significantly between seasons being almost constant throughout the year. This again indicates the importance of technology in survival for capuchins in this habitat.
- The main reward observed from tool use was the extraction of underground tubers and roots, which probably are staple resources during food bottleneck periods.
- All wild monkeys demonstrated an understanding of the causal relations of using a tool and solving a specific problem. They used tools to solve a series of ecological problems and gain access to nutritious resources. In the harsh conditions of the Caatinga, ecological pressure is suggested to be the main factor driving the cognitive abilities of *Cebus*.
- Nevertheless, capuchin populations from other Neotropical dry forest have yet to be observed using tools. These other forests probably have a higher availability of food resources than in the Caatinga. Indeed, diversity of Caatinga forest is markedly low when compared to other Neotropical dry forests and diversity can be used as a proxy for overall food availability. Tool use is emphasised as a key behavioural strategy that allows capuchin monkeys to survive in the Caatinga dry forest.



Forest by the Cliff, one of the 'green islands'.

Chapter VII

CAPUCHINS, EXTRACTIVE FORAGING AND BRAIN EVOLUTION

The Caatinga dry forest poses a series of ecological challenges for mammals in general and primates in particular. The erratic rainfall pattern (Chapter II) has a great impact on plant diversity and phenological patterns; from year to year there is a marked variability in fruit production and failure in fruiting is not uncommon (Chapter III). This harshness apparently accounts for the impoverished mammalian fauna and their generally low abundance. For primates in particular the erratic fruiting pattern coupled with low food availability has a considerable effect on group size and density by comparison to wetter habitats (Chapter IV). In the case of capuchin monkeys in general, the great bulk of their diet is composed of fruit (e.g. Freese and Oppenheimer, 1981) and food shortage could have more drastic effects on their life history and social dynamics. Edible fruits for my study group were available for a short interval, and even so only a few fruit species were present (Chapter III and V). This population faced more frequent and longer periods of food scarcity than does any other capuchin study population.

Nevertheless, in the Caatinga dry forest capuchin monkeys circumvent these ecological shortcomings through their proficient foraging style and cognitive abilities, reflected in their extensive use of technology (Chapter V and VI). The reason for *Cebus* having the highest density amongst the primates that occur in this area (Chapter IV) might be linked to the use of technology, which allowed them access to nutritious resources during food-lean times. *Alouatta caraya* (a predominantly-folivorous species) was found at extremely low density and during the dry season was

apparently confined to the canyon areas, where trees retain their leaves. The other species, *Callithrix jacchus,* has morphological feeding specialisations that allows it to gouge tree trunks for gum, an important resource during food bottlenecks periods (e.g. Ferrari and Lopes-Ferrari, 1989), yet in the harsh condition of *Caatinga* this was not sufficient to maintain them at high densities.

Capuchin, baboons and tools: extractive foraging x social brain?

The almost daily occurrence of tool use in this wild population of capuchin monkeys (Chapter VI) is in sharp contrast with the almost complete absence observed in wild groups of baboons and macaques. This is quite puzzling because baboons and macaques also occur in harsh habitats, have been observed for a much longer time than any *Cebus* population and yet records of feeding tools are virtually absent for those populations. Even in captive settings, capuchins surpass these species in tool use (Chevalier-Skolnikof, 1989). At the core of an explanation for this puzzle is the extractive foraging hypothesis, where complex food extraction is considered to be the basis for intelligent tool use and a prime reason for the evolution of a larger brain size (Parker and Gibson, 1977; Gibson, 1986). Baboons and macaques are extractive foragers and do live in habitats that poses similar or even higher ecological pressures than Caatinga. In the context of extractive foraging hypothesis it is most surprising that these non-tool using species have a larger neocortex ratio - considered as the seat of intelligence - (*Papio* spp.: 2.59-2.81 and *Macaca* spp. 2.43-2.6) than does *C. apella* (2. 25) (data from table 1 in Kudo and Dunbar, 2001).

The baboons deserve special attention for their lack of feeding tools. Tubers and roots are a staple component of their diet. Their hand morphology is appropriate for use of tools and tool manipulation, since in common with most of the other Old

World monkey species they have more fine-grained manipulative abilities than does *Cebus* (Chevalier-Skolnikoff, 1989). Baboons live in areas where rainfall can be much lower than in the Caatinga dry forest. For example in Amboseli, Kenya, the annual rainfall can be as low as 250 mm (Bronikowski and Altmann, 1996) and in Tsaobis, Namibia, in five years the mean annual rainfall was 85 mm (Cowlishaw, 1999). Yet, use of feeding tools by wild baboons is extremely rare and up to now there are just two reports; Oyen (1979) observed an adult male olive baboon using a twig to probe and extract clay fragments from the compacted soil and then eat these pellets. The second report was by Marais (1969); he observed individuals of *Papio ursinus*, in South Africa, using stones to smash hard-shelled fruits of baobab. These fruit were carried for great distances to the foot of a hill, where stones could be found and used.

Baboons have been studied intensively over the past 50 years and the lack of further observations of tool use is surprising. Perhaps, baboons have feeding adaptations that would preclude the need for tool use, as has been suggested for gorillas that are stronger and thus do not need to use feeding tools (Parker and Gibson, 1979). Indeed, Old World monkeys have a bilophodont molar that allows for a greater shearing capacity and the transit time of ingested food is much longer than in Neotropical monkeys; these adaptations allow for a better energetic gain from low quality items (Lambert, 1998; Temerin and Cant, 1983). Conversely, the tubers and roots that baboons eat could be easily located and removed without need of a tool. I could not find any reference to the density of these tuber/roots used by baboons; Altmann (1998) in his extensive and detailed study of foraging in baboons, does not provide abundance of the food resources. Even in captive settings, however, baboons and macaques in particular, perform poorly when compared to capuchin monkeys

which present tool use 50-100 times more frequently (Chevalier-Skolnikoff, 1989). Maybe the explanation for this contrast lies in differences in the brain, an evolutionary consequence of differential selective pressures on New World monkeys and Old World monkeys.

Nevertheless, the gross morphology of the capuchin monkeys' brain is much more similar to Old World monkeys than to other New World monkeys (Falk, 1989), implying that baboons, macaques and capuchin monkeys should exhibit similar abilities in tool use. The huge differences in tool use and manipulatory capabilities between capuchin monkeys and Old World monkeys (Torigoe, 1985) suggest that these species evolved different sensori-motor brain adaptations (Chevalier-Skolnikoff, 1989; Parker and Gibson, 1977).

Capuchins monkeys have a distinctive type of extractive foraging (Janson and Boinski, 1992; Chapter V), which requires a complex sensori-motor co-ordination and learning capabilities (Parker and Gibson, 1977; Gibson, 1986). It is probable that extractive foraging is the main selective pressure which explains the large brain size of capuchin monkeys and their reliance on using tools (Parker and Gibson, 1977). Recently, Rilling and Seligman (2002) found that the temporal lobe of capuchin monkeys is significantly smaller and less gyrified for a monkey with their brain size, while these areas in baboons and macaques are larger for their brain size. The temporal gyrus is involved with social communication, and these authors suggest that baboon and macaque social life is more complex, requiring a richer repertoire of verbal and non-verbal social communication. Thus, the intricacies of their social life were a selective pressure for a larger temporal lobe. Social pressure, e.g. 'Machiavellian intelligence', was a major selective pressure driving brain evolution in Old World monkeys while ecological pressures, chiefly extractive foraging might be

more prominent selective force for brain enlargement in capuchin monkeys, and this would explain their extreme proficiency in tool use. And here lies evolutionary conundrums that remain to be solved; which factors have driven brain evolution in primates, and are they the same for all primates?

Social intelligence, ecological factors and brains: revolving possibilities

Explanations for the evolution of relatively larger brains in primates are linked either to ecological factors- extractive foraging, frugivory and mental maps (Clutton-Brock and Harvey, 1980, Milton, 1981; Parker and Gibson, 1977) or to social pressures (review in Whiten and Byrne, 1988, 1997). Dunbar (1998) found no correlation between neocortex size and any of the ecological hypotheses, but a direct relationship between neocortex size and group size (see Chapter I). Nevertheless, there is an important detail that differentiates capuchin monkeys from other 'extractive foragers'; a great proportion of capuchin monkey foraging time is dedicated to extractive foraging (see Chapter I). They spend also a great proportion of their time the a more demanding extractive foraging (destructive foraging), especially breaking dead branches looking for the larvae of social insects (Janson and Boinski, 1992; Chapter V). Baboons look for insects by striping the bark off trees (Hamilton *et al.,* 1978), but to the best of my knowledge, the only other species of monkeys searching for insects inside dead branches are *Lagothrix lagotricha* and *Lophocebus albigena*. However, in marked contrast with capuchin monkeys this activity seems to be rare in these species (Poulsen *et al.,* 2001; Stevenson, 1994). Although Poulsen *et al.* (2001) state that *L. albigena* frequently broke dead branches, they did not provide frequencies or further details of this type of foraging. Dunbar (1995, 2003) stresses

that any relationships between large brain size and extractive foraging lifestyle probably were consequences of a larger brain that originated from life in large social groups, rather than the cause for enlarged brain size. If this is so, then why are there discrepancies in tool use between capuchins and other species of monkeys? Capuchin monkeys live in groups much smaller than do baboons and macaques; they lack the fluid society characterised by fission-fusion, which has been recently considered as another important evolutionary factor driving brain evolution, at least in apes (Barrett *et al.*, 2003). Among monkeys, it is the humble capuchin monkey that towers alone in tool use above the others, the only non-human primate to match the great apes in the extent of their tool use. Perhaps, the social brain hypothesis after all might not be the best explanation for these observed differences.

Some problems associated with the social brain hypothesis were already highlighted in Chapter I. A more pervasive problem is that the social brain hypothesis has been embraced like a dogma, a unitary explanation for the evolutionary enlargement of brain and thus other possibilities are not considered. Dunbar (2003) notes that despite the correlational nature of this hypothesis and an inherent weakness in drawing firm conclusions from correlation ("correlation does not equal causation"), testing between competing hypothesis can increase the explanatory power of the social brain hypothesis only if social indices correlate significantly with brain component volumes. He then confronts the social brain with alternative hypotheses for brain evolution and rebuts these alternative hypotheses. The logic of his argument cannot be faulted. But are the basic components of a complex social life (coalitions, support, use of grooming as a social currency etc.) encountered frequently in primate species with large brain size? What we know about social complexities in primates originate from a few well-studied species, namely baboons, vervet monkeys, a few

species of macaques, langurs and more recently capuchin monkeys. Moreover, what may be more important for "intelligence" *per se* is the absolute amount of tissue or number of neurons, rather than relative difference in the size of the neocortex as Gibson (2002) and particularly Gibson and Jessee (1999) have vociferously argued. More recently Russon (2004) argues that ecological pressures probably had a more prominent role shaping the cognitive evolution of great apes than did social pressures. Perhaps a more fine-grained analysis of closely-related species, but with differences in social structure, could pinpoint specific selective forces that underlie differences in cognitive abilities. Distinctiveness is a hallmark of evolutionary processes and each species, despite sharing common ancestors, will have its own peculiarities originated and shaped by specific selective forces.

Does extractive foraging account for the evolutionary brain enlargement observed in some primates? Possible, but it is extremely hard to generalise from the scanty information available. Nonetheless, when sieving through the literature I perceived that most researchers tend to stick with a single hypothesis for explaining brain enlargement. It is possible that a series of factors, not only ecological and social but also environmental, were shaping brain evolution (see Russon and Begun, 2004). The ability to conceive how these multiple selective forces worked could be hindered by our own mental limitations as the late Stephen J. Gould used to assert (e.g. Gould, 2002, p. 598: '...we are specially ill-equipped to think hierarchically, and to juggle simultaneous influences from several nested levels upon the foci of our interest').

Nonetheless, it is possible that extractive foraging has been an important selective force for brain enlargement in capuchin monkeys, leading capuchin monkeys to have a greater practical or technical intelligence, while macaques and baboons have a more social approach to solving day-to-day problems. In this sense, it

is interesting to reconsider the ideas of Parker and Gibson (1977, 1979) that extractive foraging and the dependence on tools for obtaining embedded food, which provides year-round high quality nutrition, was the initial kick for the significant brain enlargement seen in the lineage of *Homo*.

Arid environments and tool use: implications for hominid evolution

Brain-size evolution in the hominid evolutionary lineage seems to be inextricably linked to a drier habitat and increased difficulty in finding food. During the middle Miocene (16-13 Ma), there was a climatic shift to a drier phase and dry, open canopy vegetation with a grass understory spread through many lowland basins of East Africa (Retallack *et al.* 2002). This period is also a notable turning point in the terrestrial adaptations of several primate species (Retallack *et al.* 2002). The exploitation of this semi-arid environment by early hominins probably posed great cognitive demands of all kinds and selected for larger brain size. It has been argued that the exploitation of patchy resources, coupled with frugivory and a fission-fusion society were key elements selecting for larger hominin brain size and intelligence (Potts, 2004a,b). Fission-fusion society in particular has been proposed by Barrett *et al.* (2003) as a key component for explaining the differences observed at a cognitive level between monkeys and apes. However, Singleton (2004) favours the extractive foraging hypothesis as a more plausible explanation for the cognitive evolution of hominoids. To pinpoint the factors underlying brain enlargement, and those responsible for the cognitive differences between hominins, apes and monkeys, is a difficult task as discussed above and perhaps prone to mistaken speculation. Nonetheless, it is possible that the seeds of these differences were already well established before the climatic changes that occurred during the Miocene.

I suggest that the basal ancestor of all hominids had a extractive foraging style, similar to that observed in *Cebus*. With an increase in dryness of the climate during the middle Miocene, this ancestor probably used a variety of tools for improving foraging outcomes so as to meet its energetic requirements. While selective pressures led to adaptations for a low-quality diet in the ancestor of Cercopithecoidea and Colobinae, which probably originated from a more frugivorous species (Benefit, 1999), this apparently did not happen with the hominids that retained their commitment to frugivory (Potts, 2004a; Singleton, 2004). Possibly it was tool use *per se* that had the most profound impact on brain enlargement observed in hominids and particularly hominins.

The association of tool use and brain enlargement in hominins is controversial, however. For instance, Winn (1986) did not find any evidence of a relationship between the manufacture of tools and hominid brain size. He plays down tool use and technology as an important selective force driving brain evolution in hominids. Nevertheless, Stout *et al.* (2000), using brain-imaging techniques, showed that the brain areas activated during tool use and manufacture by an human too-maker are those that have undergone greatest expansion during hominid evolution. They suggest that tool use and manufacture might thus have exerted selective pressure on the early hominid brain. Perhaps the better way to examine this problem is through more comparative studies trying to understanding how the anatomy of particular brain areas are related to species-typical social behaviour, social complexities (e.g. Rilling and Seligman, 2002) or propensity for the use of technology to solve feeding problems. In this sense, the *Cebus* spp. represent a unique window into understanding the role that ecological adaptation, social pressures and environmental variables (e.g.

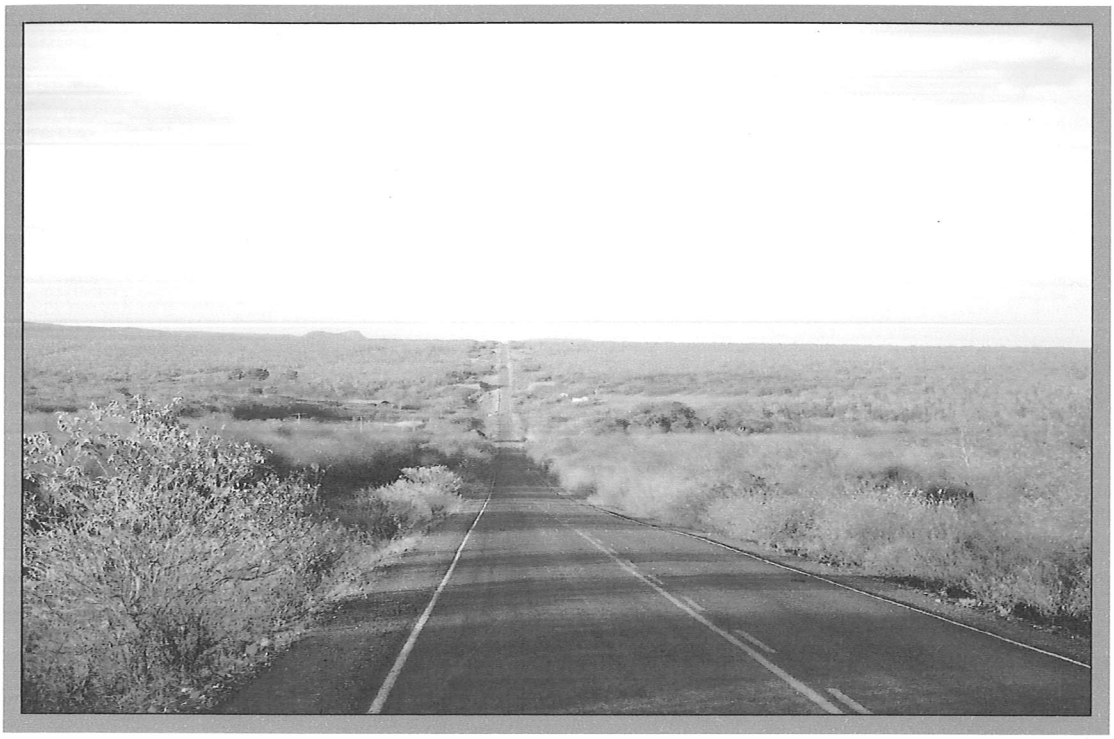
distribution of resources and seasonality) can jointly have upon the evolution of intelligence.

There are four species of *Cebus* occurring in a great diversity of habitats and presenting marked variation in their social systems (e.g. Fedigan, 1993; Jason and Robinson, 1987). For instance, *C. apella* and *C. olivaceus* exhibit a tendency to form reproductively uni-male societies, since the alpha male seems to be the only successfully-reproductive adult male (Janson, 1984; O'Brien, 1991). On the other hand, *C. albifrons* and *C. capucinus* live in multi-male groups, group sizes are bigger than in *C. apella* and *C. olivaceus*, and males exhibit low or no agonism towards other males (Defler, 1979; Fedigan, 1993; Janson, 1986). Moreover *C. albifrons* seems to be much more frugivorous than *C. apella* (Terborgh, 1983). How are these differences in social structure and levels of frugivory (or destructive foraging, e.g. Chapter V) reflected in cognitive abilities and ability to solve tool-feeding problems? Do these species present differences in specific brain areas related to larger group size or ability to use tools? Unfortunately, there is a complete absence of comparative studies on these species regarding their abilities in cognitive tasks. Interestingly, almost all of the tool use events observed in captive settings came from *C. apella;* perhaps this already could be an indication of cognitive difference among capuchin species.

Parker and Gibson (1977) pointed out that *C. apella* could be a more recent evolutionary offshoot within the genus *Cebus*. But there is not a single study on the evolutionary history of capuchin monkeys that gives an indication of which group is more basal. I suggested the possibility of *Cebus* spp. evolving in the context of drier habitats (Chapter V). It is possible that *C. apella* has undergone stronger selective pressures for drier and harsher habitats than have the other species. Unpredictability is an inherent property of drier habitats, and this could put a higher pressure on

intelligence, innovative behaviours and tool use (Lee, 2003). The failure of individuals in a wild group of *C. capucinus* to solve a tool-related problem (Garber and Brown, 2004) is significant in this context. Perhaps these species already present subtly changes in their mental machinery.

Throughout this thesis I have struggled for clarity and simplicity of reasoning, and perhaps I might be wrong in my generalisations. Nevertheless, I believe that the primate community and particularly the capuchins monkeys I observed in the Caatinga dry forest can act as a temporal window onto the evolutionary events that happened during the late Miocene in Africa, leading to the origins of intelligence in hominoids.



Nothing is forever

I whisper a poem,
A poem of nothingness!
I sing my poem,
The despair of a lone life;
An imprinting of social failure,
A stain in my soul!
This is my poem: loneliness;
An eternal emptiness.
I whisper my poem, hearing the wind;
That swiftly rocks the foliage
The wind that goes free and alone,
It carries my poem,
I stay behind like a crude and mute stone;
This is my soul,
I just whisper to the wind;
A transient emptiness!

Procrastination mood…

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APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

List of trees sampled in the different habitats of the park. C.G.= Caldeirao do Gato; B. Beti= Boqueirao da Beti; B.Oit=Boqueirao Oitenta; B. Vaca= Baixao da Vaca; Esp= Esperanca. See text in Chaper III for further details.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Anacardiaceae	*Miracroduon urundeuva*	13	X				X		
Annonaceae	*Xylopia* sp.	25		X	X			X	
Apocynaceae	*Aspidosperma* sp.	4	X						
Apocynaceae	Unknown	1							X
Bignoniace	Unknown	1	X						
Bignoniaceae	*Tabebuia impetiginosa*	197	X				X		
Bignoniaceae	*Tabebuia* cf. *serratifolia*	43	X	X			X	X	
Boraginaceae	*Cordia piahyensis*	2	X						
Boraginaceae	*C. trichotoma*	12	X				X		
Burseracaeae	*Protium* cf *heptaphyllum.*	12		X				X	
Cactaceae	*Cereus jamacaru*	7	X						
Capparaceae	*Capparis flexuosa*	22	X				X	X	
Cecropiaceae	*Cecropia* cf. *cinerea*	1					X		
Celastraceae	*Maytenus* sp.	1							X

APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

Cont.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Chrysobalanaceae	*Hirtella* sp.	1		X					
Chrysobalanaceae	*Licania octandra*	24		X		X		X	
Chrysobalanaceae	*L. tomentosa*	2					X		
Combretaceae	*Thiloa glaucocarpa*	136	X				X		
Erythroxilaceae	*Erythroxylum* sp.1	58	X	X	X	X		X	
Erythroxilaceae	*Erythroxylum* sp.2	7	X					X	
Erythroxilaceae	*Erythroxylum* sp.3	2							X
Erythroxilaceae	*Erythroxylum* sp.4	7							X
Euphorbiacea	*Cnidosculus* sp.	2							X
Euphorbiaceae	*Croton sonderianus*	76	X				X	X	
Euphorbiaceae	*Manihot cf. glaziovii.*	8							X
Euphorbiaceae	*Sapium* sp.	2	X						
Flacourtiaceae	*Prockia crucis*	25	X				X	X	
Lauraceae	*Ocotea* sp.1	107		X			X	X	
Lauraceae	*Ocotea* sp.2	7	X	X	X				

APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

Cont.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Leg Ceaesalpiniaceae	*Caesalpinia. bracteosa*	18	X						
Leg Ceaesalpiniaceae	*C. ferrea*	3	X				X	X	
Leg Ceaesalpiniaceae	*Cenostigma gardnerianum*	54	X						X
Leg Ceaesalpiniaceae	*Copaifera* cf. *langdorsfii*	6	X						
Leg Ceaesalpiniaceae	*Hymenaea aurea*	14							X
Leg Ceaesalpiniaceae	*Hymenaea courbaril*	11	X				X		
Leg Ceaesalpiniaceae	*Cassia eitenorum*	82							X
Leg Ceaesalpiniaceae	*Senna spectabilis*	150	X				X	X	
Leg Ceaesalpiniaceae	Unknown sp.1	37	X						
Leg Ceaesalpiniaceae	Unknown sp.2	1	X						
Leg Ceaesalpiniaceae	Unknown sp.3	7							X
Leg Fabaceae	*Andira* sp.	33	X	X					
Leg Fabaceae	*Bauhinia cheilanta*	30	X			X			
Leg Fabaceae	*Bauhinia* sp.1	9							X
Leg Fabaceae	*Bauhinia* sp. 2	16	X					X	
Leg Fabaceae	*Bocoa mollis*	1							X

APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

Cont.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Leg Fabaceae	*Dalbergia* sp.	11	X						
Leg. Fabaceae	*Lonchocarpus* sp.	4							X
Leg Fabaceae	*Pterodon abruptus*	58							X
Leg Fabaceae	*Swartzia flamengii*	9	X						X
Leg Mimosaceae	*Acacia cf. langsdorfii*	42							X
Leg Mimosaceae	*Acacia* cf. *paniculata*	13					X	X	
Leg Mimosaceae	*Acacia* sp.	1					X		
Leg Mimosaceae	*Anadenanthera colubrina*	98	X						
Leg Mimosaceae	*Chloroleucon* cf. *dumosum*	6	X				X	X	
Leg Mimosaceae	*Diptychandra epunctata*	6							X
Leg Mimosaceae	*Enterolobium contortisiliiqum*	2	X						
Leg Mimosaceae	*Inga aff. capitata*	34		X				X	
Leg Mimosaceae	*Mimosa acutistipula*	28	X				X		
Leg Mimosaceae	*M. lepidophora*	15							X
Leg Mimosaceae	*M. tenuiflora*	6	X				X	X	
Leg Mimosaceae	*Piptadenia biuncifera*	4					X	X	

APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

Cont.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Leg Mimosaceae	*Piptadenia obliqua*	42	X	X					X
Leg Mimosaceae	*P. stipulacea*	26	X				X	X	X
Malphighiaceae	*Byrsonima* sp.	8							X
Malphighiaceae	*Ptylochaeta* sp.	18	X						
Meliaceae	*Trichilia hirta*	56	X	X			X	X	
Meliaceae	*Trichilia* sp.	24			X	X			
Moraceae	*Brosimum* cf. *alicastrum*	7	X	X		X			
Moraceae	*Ficus gomelleira*	7	X				X	X	
Myrsinaceae	*Cybianthus* sp.	8		X				X	
Myrtaceae	*Eugenia* sp. 1	207	X	X	X	X		X	
Myrtaceae	*Eugenia* sp.2	17			X				
Myrtaceae	*cf. Eugenia* sp.	47	X				X		X
Myrtaceae	*Myrcia* sp.	28	X	X	X	X	X	X	
Myrtaceae	Unknown sp.1	20							X
Myrtaceae	Unknown sp. 2	34							X
Myrtaceae	Unknown sp.3	1						X	

APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

Cont.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Myrtaceae	Unknown sp.4	3				X		X	
Myrtaceae	Unknown sp.5	2			X				
Myrtaceae	Unknown sp.6	10		X		X	X	X	
Myrtaceae	Unknown sp.7	3				X			
Myrtaceae	Unknown sp.8	2		X					
Myrtaceae	Unknown sp.9	4							X
Nyctaginaceae	*Guapira* sp.	24							X
Nyctaginaceae	Unknown sp.	1				X			
Ochnaceae	*Ouratea castanaefolia*	30		X			X	X	
Olecaceae	*Ximenia americana*	3							X
Rhamnaceae	*Colubrina cordifolia*	1							X
Rhamnaceae	*Zizyphus joazeiro*	34	X				X	X	
Rubiaceae	*Alibertia* sp.	8			X				
Rubiaceae	*Guettarda* sp.	23	X				X	X	
Rubiaceae	*Rhandia armata*	13					X	X	

APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

Cont.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Rubiaceae	*Tocoyena formosa*	3	X		X				
Rutaceae	*Fagara* sp.	43	X	X	X	X	X	X	
Rutaceae	*Pilocarpus* sp.	6							X
Rutaceae	*Zanthoxylum hamadryadicum*	2							X
Sapindaceae	*Allophylus* sp.	33					X	X	
Sapindaceae	*Talisia esculenta*	165	X	X			X	X	
Sapotaceae	*Chrysophillum* sp.	9			X	X			
Sapotaceae	*Pouteria* sp.1	29	X				X	X	
Sapotaceae	*Pouteria* sp.2	105	X				X	X	
Sapotaceae	Unknown sp.	4				X		X	
Simaroubaceae	*Simarouba* sp.	7					X		
Solanaceae	*Solanum* sp.1	4						X	
Solanaceae	*Solanum* sp.2	2	X						
Sterculiaceae	*Helicteres* sp.	1						X	
Styracacea	*Styrax* sp.	4		X					
Ulmaceae	*Trema micrantha*	2					X	X	
Vitaceae	*Vitex sp.*	14			X				

APPENDIX 1 – CHECK LIST OF TREES SAMPLED IN THE PARK

Cont.

Family	Species	Frequency	Cliffs	C. G.	B. Beti	B. Oit	B. Vaca	Esp	Plateau
Unknown	Unknown sp. 1	1			X				
Unknown	Unknown sp.2	1	X						
Unknown	Unknown sp. 3	3					X		
Unknown	Unknown sp. 4	2					X		
Unknown	Unknown sp. 5	1						X	
Unknown	Unknown sp. 6	1		X					
Unknown	Unknown sp. 7	1		X					
Unknown	Unknown sp. 8	1				X			
Unknown	Unknown sp. 9	2							X
Unknown	Unknown sp. 10	1							X
Unknown	Unknown sp. 11	1							X
Unknown	Missing (> than one sp.)	13							X

APPENDIX 2 – TREE DIVERSITY IN THE NEOTROPICS

Tree diversity in 0.1 ha plots in the Neotropical dry forests.

Location	# of individuals	# of species	Rainfall (mm)	Source	Calculated Fisher's α
Pueto Rico- Guanica	1217	34	860	Gentry (1995)	6.489
Pueto Rico- Mogotes	418	37	1500	"	9.797
Jamaica- Round hill	659	48	1200	"	11.91
Jamaica- Round hill	557	54	1200	"	14.77
Mexico- Chamela I	357	79	748	"	31.41
Mexico- Chamela II	451	80	748	"	28.26
Mexico- Chamela III	311	81	748	"	35.59
Costa Rica- Guanacaste I	356	47	1600	"	14.5
Costa Rica- Guanacaste II	171	55	1600	"	28.08
Costa Rica- Santa Rosa	169	54	1552	Gillespie (1999)	27.43
Costa Rica- Palo Verde	183	47	1717	"	20.46
Nicaragua- Cosiguina	118	38	1827	"	19.42
Nicaragua- Masaya	223	33	1251	"	10.7
Nicaragua- Chacocente	177	43	1362	"	18.08
Nicaragua- La flor	202	45	1805	"	17.96
Nicaragua- Ometepe	106	26	1695	"	11
Argentina- Salta	193	22	712	Gentry (1995)	6.39
Argentina- Riachuelo	339	39	1200	"	11.38
Argentina- El Rey	146	31	1500	"	12.04
Bolivia- Chaquimayo	331	50	1300	"	16.37
Bolivia- Santa Cruz	107	36	1171	"	19.05
Bolivia- Quiapaca	277	55	?	"	23.08
Colombia- Bolivar	292	36	500	"	10.08
Colombia- Magdalena	238	49	1500	"	18.71
Colombia- Bolivar	383	81	770	"	31.39
Colombia- Tolima	299	56	?	"	20.33
Colombia- Sucre	238	75	?	"	37.69
Venezuela- Boca de Uchire	222	53	1200	"	22.04
Venezuela- Los Llanos	274	49	1312	"	17.38
Venezuela- Blohm Ranch	230	51	1400	"	20.03
Ecuador- Guayas	243	42	804	"	14.65
Ecuador- Manabi	272	54	1000	"	20.22
Peru- Tumbes	377	43	1430	"	12.05
Peru- San Martin	434	75	1400	"	26.15
Venezuela- Iguez	375	45	?	Stergios *et al.*1998	13.35
Venezuela- Rio	395	41	?	"	11.5
Venezuela- Delgadito	398	41	?	"	11.47

APPENDIX 3 – GROUP SIZE, USE OF SPACE AND DENSITY IN *CEBUS APELLA*

Group size in *Cebus apella* inhabiting different types of habitats within their geographical range. Am= Amazonian Forest; At= Atlantic Forest; Ll= Llanos semi-deciduous forest; Sbt= Sub-tropical Atlantic forest from Northern Argentina.

Forest type	Mean group size	Number of groups	Home-range (ha)	Density Individuals /km^2	Source
Ll- Colombia	6	1	~ 90		Defler (1982)
Ll- Colombia	11	1	~ 90		"
Ll- Colombia	12	1	~ 90	13.3	"
Am- Terra firme	16	1	260	6.1	Izawa (1980)
Am- Guyan shield	13	1	355	3.66	Zhang (1995)
Am- Terra firme	14	1	852	1.6	Spironello (2001)
Am- Cocha Cashu	10	1	80	12.5	Terborgh (1983)
Am- Cocha Cashu	16	1	?	--	Van Schaik and Noordwijk (1989)
Am- Cocha Cashu	14	1	?	?	Janson (1984)
Am- Cocha Cashu	11	1	?	?	"
Am- Cocha Cashu	7	1	?	?	"
Am- Cocha Cashu	3	1	?	?	"
Sbt- Argentina	22	1	?	?	Janson and Di Bitetti (1997)
At- Rainforest	13	1	?	2.3	Izar (2004)
Am-Varzea forest	6.7	4	?	24.1	Peres (1988)
Am-Varzea forest	7	1	?	14.6	"

APPENDIX 3 – GROUP SIZE, USE OF SPACE AND DENSITY IN *CEBUS APELLA*

Cont..

Forest type	Mean group size	Number of groups	Home-range (ha)	Density Individuals /km^2	Source
Am-Terra firme	8	3	?	15	Peres (1988)
Am-Terra firme	7	1	?	6.8	"
Am-Terra firme	7	1	?	6.7	"
Am-Terra firme*	16.3	7	250	32.3	Peres (1993)
At- semideciduous?	6.5	15	?	10.2	Pinto *et al.* (1993)
At- semideciduous?	8	4	?	26.4	Price *et al.*(2002)
At- semideciduous?	6.29	7	?	--	Chiarello (1997)

APPENDIX 4 – ENCOUNTER RATE AND DENSITY OF *CEBUS APELLA*

Encounter rate (groups/ 10km) of *Cebus apella* in different types of habitats within their geographical range. Am= Amazonian Forest; At= Atlantic Forest; DS= Distance sampling program; OT= King's, Leopold's method or other type of density estimator.

Forest type	Encounter rate	Density Individuals /km^2	Density estimator	Source
Am -Terra firme	0.2	2.9	DS	Peres (1997a)
Am -Terra firme	0.6	9	DS	"
Am -Terra firme	1	15.7	DS	"
Am -Terra firme	1.5	24.8	DS	"
Am -Terra firme	0.8	12.9	DS	"
Am -Terra firme	3	49.6	DS	"
Am -Terra firme	2.4	28.3	DS	"
Am -Terra firme	2.3	38.2	DS	"
Am -Terra firme	0.5	7.8	DS	"
Am -Terra firme	1.3	21	DS	"
Am -Terra firme	0.8	12.4	DS	"
Am -Terra firme	0.7	12.7	DS	"
Am – Varzea	1.1	17.4	DS	"
Am – Varzea	2.9	55.7	DS	"
Am – Varzea	3.3	53.7	DS	"
Am – Varzea	1.3	21.4	DS	"
Am – Varzea	1.3	20.1	DS	"
Am- Flooded forest	0.9*	11.5	DS	Bennett *et al.* (2001)
Am- Flooded forest	1.5*	20.15	DS	"
Am -Terra firme	1.06	14.1	DS	Wallace *et al.* (1998)

APPENDIX 4 – ENCOUNTER RATE AND DENSITY OF *CEBUS APELLA*

Cont.

Forest type	Encounter rate	Density Individuals /km^2	Density estimator	Source
At- semi-deciduous	1.24	10.93**	DS	Cullen *et al.* (2001)
At- semi-deciduous?	2.47	25.76	DS	Chiarello (1999)
At-semi-deciduous?	1.51	15.8	DS	"
At-semi-deciduous?	1.05	11.01	DS	"
At-semi-deciduous?	0.6	6.25	DS	"
At-semi-deciduous?	2.19	21.36	DS	Chiarello (1999)
At-semi-deciduous?	1.23	11.45	DS	"
At-semi-deciduous?	0.905	1.6	OT	Pinto *et al.*(1993)
Am- Guyanan shield	0.17	--		Lehman (2000)
Atl- semi-deciduous?	1.13	22	OT	Price *et al.* (2002)
Am- Terra firme	0.69	8.2	OT	Thoysi (2000)

*Encounter rate was individuals/10km, I calculated these from the average group size provided by the author.

** The density is the average density from the values provided by the authors

APPENDIX 5 – LIST OF PLANTS CONSUMED BY CAPUCHIN MONKEYS IN THE STUDY SITE

List of species of plants consumed by *Cebus apella libidinosus* in the study site. Life form: T= tree, C= cactus, h= herb; V= vine, G= grass. Part eaten= P=pith, F= fruit, FL=flower, T= tuber, S= seed predation. The list was based from direct observation and from seeds found in the collected dungs.

Species	Life form	Part eaten
Anadenanthera colubrina	T	P; F
Bromelia plumieri	H	F
Brosimum cf. *alicastrum*	T	F
Caesalpinia bracteosa	T	P
Capparis flexuosa	T	P; F; FL
Cereus jamacaru	C	P
Copaifera cf. *langsdorfii*	T	F
Enterolobium cf *contortisiliquum*	T	P
Eremanthus martii	H	P
Erythroxylum sp.1	T	F
Erythroxylum sp.2	T	F
Eugenia sp.1 .	T	F
Ficus gomeleira	T	F
Hymenaea courbaril	T	P; F
Inga aff. capitata	T	F
Ipomea sp.	V	Tb
Laseis sp*.	G	S
Leguminosae unknown	V	P
Manihot glaziovii	T	S
Miracroduon urundeuva	T	P
Myrtaceae	T	F
Pilosocereus piauhyinsis	C	P
Pouteria sp.1	t	P; F?
Pouteria sp. 2	T	P;F?
Prockia crucis		F
Ruellia sp.	H	FL
Tabebuia cf *serratifolia*	T	P; F
Tabebuia impetiginosa	T	P
Tabebuia spongiosa	T	Fl
Talisia sculenta	T	F
Thiloa glaucocarpa	T	T;P
Trichilia sp.	T	F
Vitex sp.	T	F
Zizyphus joazeiro	T	F
Unknown sp. 1	?	F
Unknown sp.2	?	F
Unknown sp.3	?	F
Unknown sp.4	?	F
Unknown sp.5	?	F
Unknown sp.6	?	F

APPENDIX 6 - TOTAL SCANS AND OBSERVATION HOURS

Total scans and observation hours for the Oitenta group

Month	Number of Scans	Hours of obs.	*Ad libitum*
Oct-00			15.00
Nov-00	42	21.00	09:35
Dec-00	46	23.00	01:40
Jan-01	68	34.00	04:39
Feb-01	44	22.00	00:55
Mar-01	70	35.00	00:40
Apr-01	60	30.00	
May-01	27	13.50	
Jun-01	55	27.50	
Jul-01	71	35.50	
Aug-01	67	33.50	
Sep-01	51	25.50	
Oct-01	40	20.00	
Nov-01	37	18.50	
Dec-01	24	12.00	
Jan-02	16	8.00	
Feb-02			0.19
Mar-02			2.20
TOTAL	**718**	**359**	**33.48**

Total minutes of focal animal sampling.

Individuals	Wet season	Dry season	Total
Boludo	183	170	353
Wfemale	166	186	352
Cara-branca	128	150	278
Peta	138	140	278
Desc.	126	109	235
Adtmale	100	139	239
Clarinha	85	146	231
TOTAL MINUTES	**926**	**1,040**	**1,966**